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CONTENTS

GESS, F. W. The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part I. Descriptions of new species with complete venation 211

GRISSELL, E. E. Torymidae (Hymenoptera: Chalcidoidea) associated with bees (Apoidea), with a list of chalcidoid bee parasitoids 234

NEFF, J. L. and A. W. HOOK. Multivoltinism and usage of multiple nest substrates in a west Texas sand dune population of *Pseudomasaris phaceliae* Rohwer (Hymenoptera: Vespidae: Masarinae) 266

PACKER, L. *Mydrosoma micheneri* Packer, new species, a new diphaglossine bee from Brazil (Hymenoptera: Colletidae) 277

PACKER, L., A.-I. D. GRAVEL, and G. LEBUHN. Phenology and social organization of *Halictus* (*Seladonia*) *tripartitus* (Hymenoptera: Halictidae) 281

PULAWSKI, W. J. The status of *Liris magnificus* Kohl, 1884, and *Trachogorytes costaricae* R. Bohart, 2000 (Hymenoptera: Crabronidae: Crabroninae, Bembicinae) 293

PUNZO, F. Interspecific variation in hunting behavior of *Pepsis grossa* (Fabricius) and *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae): a field study 297

SHIMIZU, A. and R. WAHIS. Systematic studies on the Pompilidae occurring in Japan: genus *Irenangelus* Schulz (Hymenoptera: Pompilidae: Ceropalinae) 311

WENG, J. L. and BARRANTES, G. Natural history and larval behavior of the parasitoid *Zatypota petronae* (Hymenoptera: Ichneumonidae) 326

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The Genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part I. Descriptions of New Species with Complete Venation

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Abstract.—In this publication, the first of a projected series revising the Afrotropical (essentially southern African) species of the genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae, Masarinae), eleven new species are described. Of these, seven occurring variously in the southern Namib Desert and in its southward extension down the western coast of South Africa, and one occurring on the southern coast of South Africa, have been found nesting in sand-filled snail shells. They are: ***australis***, ***bonaespei***, ***conchicola***, ***namaqua***, ***namaquensis***, ***obibensis***, and ***refugicola***. To these species is added ***vexillata*** which is presumed to have the same nesting habits. A key to distinguish these species is given. The other three newly described species, all from Namibia, are: ***femorata***, ***geigeriae*** and ***lamellata***.

Following van der Vecht and Carpenter (1990) *Quartinia* Ed. André, 1884 is here understood to include, as junior subjective synonyms, *Quartiniella* Schulthess, 1929 and *Quartinioides* Richards, 1962.

As has been pointed out by Carpenter (2001), *Quartiniella* and *Quartinioides* were primarily based on the partitioning of a trend in the reduction of wing venation, *Quartiniella* being defined on the basis of the loss of 3*rs-m* and 2*m-cu* and *Quartinioides* because it has 2*m-cu* present but attenuate and interrupted, whereas *Quartinia* has it complete. In *Quartiniella* in particular and to some extent also in *Quartinioides* reduction of wing venation is a correlate of overall size reduction As formal taxonomic partitioning of essentially continuous variation is an unacceptable practice, Carpenter synonymized *Quartiniella* and *Quartinioides* with *Quartinia*, a view with which the present author is in full agreement.

Nevertheless, in view of the large number of species in *Quartinia*, adoption of the above venational characters to divide the genus into smaller, more manageable but totally informal, non-natural units is found to be useful. Thus the present paper deals with species with complete venation – that is species which in the past would have been placed in *Quartinia sensu stricto*.

In his revision Richards (1962) dealt with a total of 61 southern African species, 18 being placed in *Quartinia*, 38 in *Quartinioides* and five in *Quartiniella*. Of these, 11, 26 and two respectively were described as new. One additional species, placed in *Quartinioides* was added (Richards 1982). Available to Richards in 1962 were just over one thousand specimens – 140 *Quartinia*, 727 *Quartinioides* and 148 *Quartiniella*. Ten species were known from only one specimen, 30 species from only one sex. It is clear that Richards suffered from a paucity of material. Particularly the lack of large samples from individual populations spread over the distributional area prevented him from appreciating factors such as intraspecific variation and geographical clines. In some instances the associations of sexes is of doubtful validity, especially where males and females are from widely separated localities.

The present study is based on over 6000 specimens, most of which were purposefully collected. A large proportion of the specimens have associated biological data – mostly flower visiting records but also, for some species, nesting data.

Desirable as it might be to undertake a complete revision of the genus, this is at present not practicable. Rather than to get bogged down in a study which might never be completed and published, it is intended to publish a series of papers describing new species as well as reviewing some known species. It is envisioned that a new key to species will complete the series.

Quartinia species range in length from a little over 2 mm to 7 mm. In comparison with the great majority of species of other genera of Masarinae even the largest *Quartinia* are relatively small. In view of the considerable range in size shown by species of *Quartinia* and in order to express relative size, categories based on length have been established for species of the genus. These are: minute (1.5–2.5 mm); small (2.5–3.5 mm); medium (3.5–4.5 mm); large (4.5–5.5 mm); very large (5.5–6.5 mm); and gigantic (6.5–7.5 mm).

The notation used for expressing geographic co-ordinates is as in the gazetteer of *The Times Atlas of the World* (1981). The figures before the stop are degrees, those after the stop are minutes; the stop is **not** a decimal point.

For purposes of plotting distributions, co-ordinates have been given in square brackets in the text for those localities for which none are given on the data labels.

On a few data labels from collections other than that of the Albany Museum the collecting locality is followed by degree latitude and degree longitude and by half- and quarter-degree reference letters according to the Degree Reference System of Leistner and Morris (1976). As this system is not universally understood an attempt has been made here to find on a map the localities concerned and to add in square brackets the co-ordinates expressed in the manner adopted in this paper.

In listing the material examined, the localities have been arranged, as far as practicable, in north to south order within countries or, in the case of South Africa, within provinces.

Acronyms for institutions in which material is housed are: AMG = Albany Museum, Grahamstown, South Africa; CAS = California Academy of Sciences, San Francisco, United States of America; FSCA = Florida State Collection of Arthropods, Gainesville, United States of America; NCP = National Collection of Insects, Pretoria, South Africa; NNIC = Namibian National Insect Collection, Windhoek, Namibia.

DESCRIPTION OF SPECIES AND COLLECTION DATA

A) Species nesting in sand-filled snail shells or (*vexillata*) presumed to do so.

Quartinia australis Gess, new species

Diagnosis.—Large (5.0–5.4 mm). Fore wing with Cu1a and *2m-cu* complete and as thick as the other veins. Tegula with posterior inner corner inwardly produced. Both sexes predominantly black with limited white markings; male with clypeal disc and underside of scape and pedicel white.

Description.—Female: Black. The following are white: narrow anterior margin of pronotum (in most specimens) and extreme postero-dorsal angle of same; tegula anteriorly and posteriorly; lateral lamella of scutellum; posterior bands medially on terga I–V (that on V in some specimens reduced to a postero-medial spot); distal end of fore femur; streaks on fore and middle tibiae; proximal and distal ends of hind tibia. Brown are: rest of legs; underside of flagellum. Wings lightly browned.

Length 5.0–5.4 (average of 5:5.3 mm); length of fore wing 3.4–3.6 mm (average of 4:3.53 mm); hamuli 6.

Head in front view 1.31 × as wide as long, finely microreticulate, matt; clypeus apunctate; frons and vertex with shallow punctures separated by about their width (punctures barely perceivable on lower regions of frons, clearer in ocular sinuses and upper part of frons and particularly on vertex. POL:OOL = 1:0.6. Clypeus 1.5 × as wide as long; anterior margin shallowly and widely emarginate; antero-lateral angles rounded.

Mesosoma microreticulate, moderately shiny, with punctures larger and more obvious than on head.

Gaster microreticulate but shiny; punctures finer and shallower than on head and much more so than those on mesosoma, becoming progressively finer posteriorly.

Male: Black. White markings as in female, with in addition: labrum; disc of clypeus (i.e. not sides nor areas adjacent to antennal sockets); underside of scape and pedicel; posterior band on tergum VI; distal end of middle and hind femora. Underside of flagellum white suffused with reddish-brown.

Length 5.0–5.4 (average of 4:5.1 mm); length of front wing 3.4–3.6 mm (average of 4:3.42 mm); hamuli 6.

Head in front view 1.5 × as wide as long; POL:OOL = 1:0.6. Clypeus 1.5 × as wide as long; anterior margin shallowly and widely emarginate; antero-lateral angles rounded.

Microsculpture and punctuation of head and body similar to that of female.

Tergum VII (Fig. 6) with surface noticeably depressed and with hindmargin with a short median slit. Sterna I–VI unmodified; sternum VII trilobed, basally markedly concave between swollen and posteriorly produced lateral lobes and with median lobe flat and densely setose.

Etymology.—The name *australis* draws attention to the southern provenance of the species.

Material examined.—Holotype: ♂, SOUTH AFRICA: WESTERN CAPE: Witsand (34.23S 20.52E), 14.viii.2002 (F. W. and S. K. Gess) (ex nest in shell of *Theba pisana* (Müll.), Helicidae) [AMG]. Paratypes: SOUTH AFRICA: WESTERN CAPE: same data as holotype, 7 ♀♀, 4 ♂♂ (ex nests in shells of *Theba pisana* (Müll.), Helicidae) [AMG].

Geographic distribution.—Known only from the type locality, Witsand, near Port Beaufort at the mouth of the Breë River, a little to the west of the southernmost point of Africa.

Floral associations.—Unknown.

Nesting.—Found nesting in sand-filled shells of the exotic *Theba pisana* (Müll.) (Mollusca: Gasteropoda: Pulmonata: Helicidae) collected from the surface of the sand below bushes growing on supralittoral dunes.

Quartinia bonaespei Gess, new species

Diagnosis.—Very large to gigantic (6.3–7.0 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula short, laterally rounded, with posterior inner corner inwardly produced. Both sexes black with white-marked pronotum, tegula and scutellar lamella and with wide, bright reddish-orange posterior bands on all but last two terga. Male with greatly enlarged and modified fore leg, with somewhat modified middle and hind legs, with tergum VII apico-medially drawn out into a robust, dorsally flattened and apically rounded process, and with sterna medially depressed.

Description.—Female: Black. The following are white: medially interrupted transverse band on dorsum of pronotum and minute dot at postero-dorsal angle of same; anterior and posterior thirds of tegula (median third black); medially broadly interrupted band on lamellate margin of scutellum. Bright reddish-orange are: mandibles distally; posterior markings dorsally (i. e. not extending down sides) on terga I–IV (that of tergum I wide, covering entire dorsal surface, that of II slightly narrower, that of III wide medially but narrowed laterally, that of IV a median

transverse spot). Labrum brown. Underside of antennae, to various degrees, pale. Coxa, trochanter, femur and tibia of all legs black with exception of yellowish streak on antero-dorsal surface of fore tarsus and same colour on extreme base of middle and hind tibiae; tarsomeres dark brown. Wings brown; veins dark brown to black.

Length 6.3–7.0 mm (average of 5:6.7 mm); length of fore wing 4.3–4.5 mm (average of 5:4.4 mm); hamuli 6.

Head in front view 1.29 × as wide as long, microreticulate, matt, with small, shallow punctures (sparse on clypeus, well separated on lower part of frons but progressively closer on upper part of frons and on vertex). POL:OOL = 1:0.75. Clypeus 1.3 × as wide as long; anterior margin shallowly emarginate; antero-lateral angles rounded.

Mesosoma microreticulate, matt, with punctures slightly larger and deeper than on head (moderately well separated on mesoscutum and scutellum, closer on pronotum and upper part of mesopleuron where sculpture almost reticulate-punctate).

Gaster microreticulate but shiny; punctures finer and shallower than on head and mesosoma, becoming progressively finer posteriorly.

Male: Black. White markings as in female. Bright reddish-orange markings on gaster similar to those of female but present also on tergum V where transverse as on anterior terga. Underside of flagellomeres, antero-distal spot on fore femur, dorsal and anterior surfaces of fore tibia, fore tarsus, yellowish-orange.

Length 6.3 mm; length of fore wing 4.6 mm; hamuli 6.

Head in front view 1.33 × as wide as long, much more finely microreticulate and much more finely punctate than in female, moderately shiny. POL:OOL = 1:0.7. Clypeus shorter than that of female, 1.46 × as wide as long.

Mesosoma much more finely microreticulate and much more finely punctate than in female, moderately shiny.

Fore leg much modified; coxa and trochanter enlarged; femur (Fig. 1) greatly swollen, postero-basally with pointed tubercle, its posterior surface depressed, smooth and very shiny and forming an angle with ventral surface; tibia greatly enlarged, ventrally with its swollen basal section fitting into opposing disto-ventral emargination of femur (best seen in anterior view); tarsomeres robust, noticeably setose. Middle and hind legs more robust than those of female; femora of both these legs swollen beneath but longitudinally grooved over distal half to accommodate tibia when opposed; tarsomeres II–IV of middle leg noticeably wider than those of hind leg.

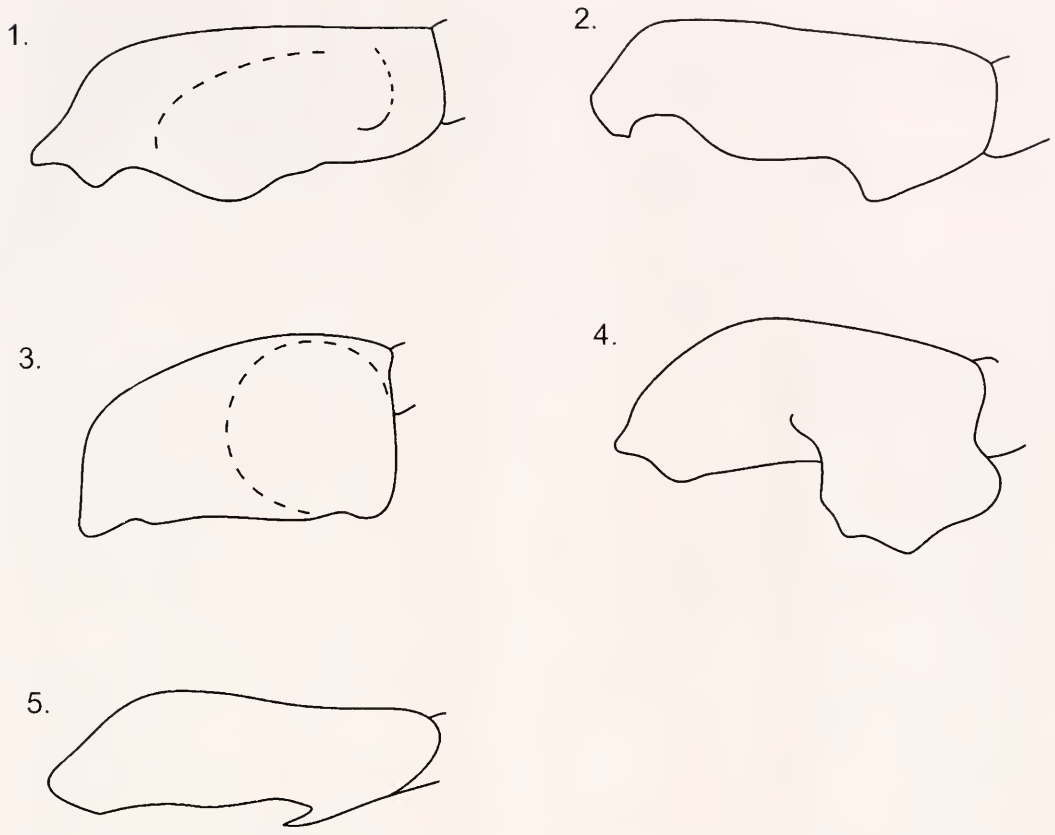
Gaster very finely microreticulate, shiny.

Tergum VII (Fig. 7) baso-laterally with a pronounced rounded tubercle, apico-medially drawn out into a robust, dorsally flattened and apically rounded process raised above depressed surface on either side of it; process dorsally with a slight median longitudinal carina and laterally on each side with a smooth low carina (carried forward some distance onto the tergal disk) at angle formed by its dorsal and lateral surfaces; hind margin of tergum in lateral view forming a low smooth curve from basal tubercle to tip of apical process.

Sternum II–VI depressed medially; sternum II markedly so; III–VI progressively less so.

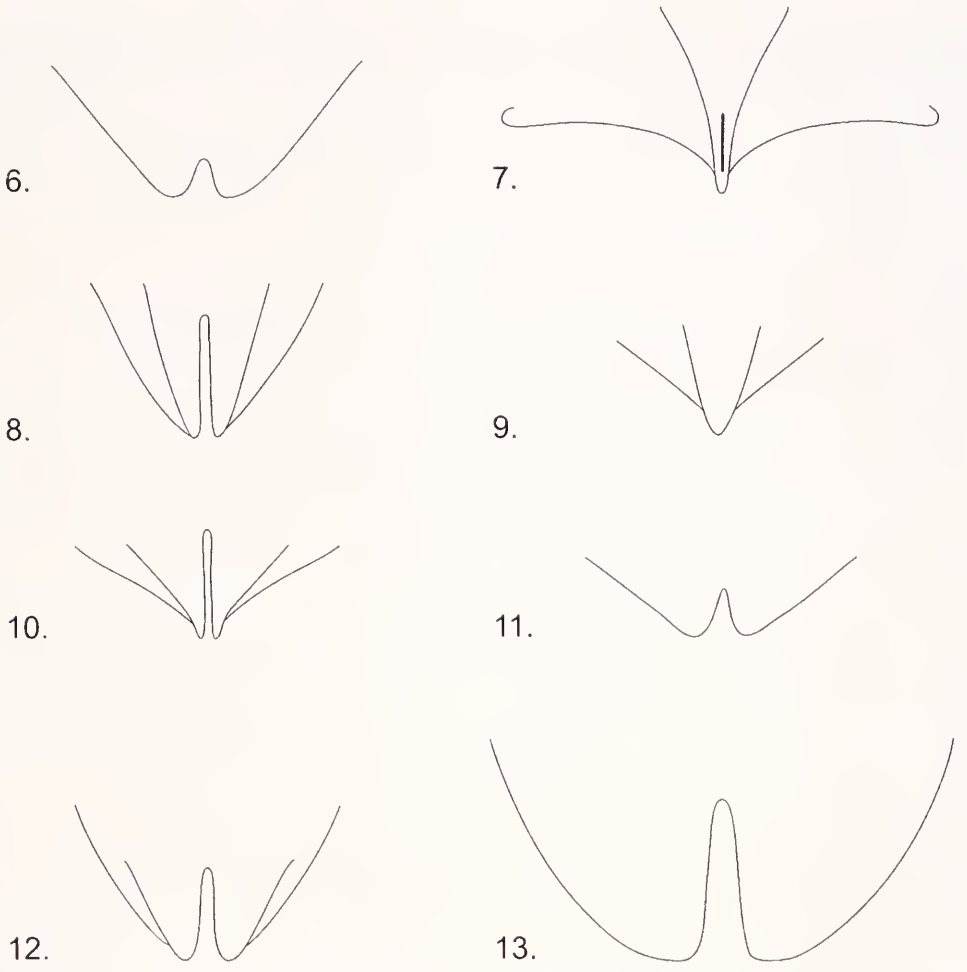
Etymology.—The name *bonaespei*, a Latin noun in the genitive, refers to the Cape of Good Hope and draws attention to the provenance of the species, especially to the type locality which is within sight of Table Mountain.

Material examined.—Holotype: ♂, SOUTH AFRICA: WESTERN CAPE: on coast 4 km north of Bloubergstrand (33.46S 18.27E), 12–13.viii.2002 (F. W. and S. K. Gess) (on ground) [AMG]. Paratypes: SOUTH AFRICA: WESTERN CAPE: Donkinsbaai, 10 km S of Doornbaai, low vegetated dunes and slacks behind beach (31.54S 18.17E), 9.ix.2005 (F. W. and S. K. Gess), 8 ♀♀ (4 ♀♀ from sand-filled *Trigonephrus*



Figs. 1–5. Left fore femur of male (posterior view). 1. *Quartinia bonaespei*, 2. *Quartinia conchicola*, 3. *Quartinia namaquensis*, 4. *Quartinia vexillata*, 5. *Quartinia femorata*.

shells; 2 ♀♀ reared from mature larvae ex *Quartinia* nests ex sand-filled *Trigonephrus* shells, emerged in lab. first week of June 2006; 2 ♀♀ visiting white centred, pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembryanthema) [AMG]; Lamberts Bay, dunes behind beach (32.05S 18.19E), 28.ix.2005 (F. W. and S. K. Gess), 1 ♀ (from *Trigonephrus* shell) [AMG]; Lamberts Bay, sandy southern bank of lagoon (32.05S 18 19E), 28.ix.2005 (F. W. and S. K. Gess), 3 ♀♀ (visiting yellow flowers of *Conicosia*, Aizoaceae: Mesembryanthema) [AMG]; Elands Bay, low vegetated dunes behind beach (32.19S 18.20E), 30.ix.2005 (F. W. and S. K. Gess), 3 ♀♀, 1 ♂ (1 ♀ from sand filled *Trigonephrus* shell; 2 ♀♀ visiting pink flowers of *Drosanthemum*, Aizoaceae: Mesembryanthema; 1 ♂ reared ex *Quartinia* nest in sand-filled *Theba pisana* (Müll.) shell, emerged in lab. 6.viii.2006) [AMG]; Roscherpan Nature Reserve (32.36S 18.18E), 24.iii.2001 (Feuerer & Thell), 4 ♀♀, 1 ♂ (from shells of *Trigonephrus porphyrostoma* (Melvill & Ponsonby) [Zool. Mus Berlin]; Yzerfontein (33.20S 18.10E), 15.x.2006 (D. W., G. T. and G. M. Gess), 1 ♀ (ex *Theba pisana* shell) [AMG]; S of Yzerfontein (33.22S 18.11E), 15.x.2006 (D. W., G. T. and G. M. Gess), 1 ♀ (on sand) [AMG]; Melkbosstrand (33.42S 18.26E), 10.x.2005 (F.W. and S. K. Gess), 2 ♀♀ (1 ♀ on sand beneath flowering *Trachyandra divaricata* (Jacq.) Kunth., Asphodelaceae; 1 ♀ reared from mature larva ex *Quartinia* nest ex sand-filled *Theba pisana* shell) [AMG]; on coast 4 km north of Bloubergstrand (33.46S 18.27E), 12–13.viii.2002 (F. W. and S. K. Gess), 11 ♀♀, (6 ♀♀, 3 ♀♀ visiting white flowers of *Trachyandra divaricata*; 1 ♀ visiting purplish pink flowers of Aizoaceae: Mesembryanthema; 1 ♀ ex nest in sand-filled *Trigonephrus* shell) [AMG]; same locality, 5.x.2005 (F. W. and S. K. Gess), 4 ♀♀, 1 ♂ (1 ♀ from sand filled *Trigonephrus* shell; 1 ♀ visiting white flowers of *Trachyandra divaricata*; 2 ♀♀ on sand beneath flowering *Trachyan-*



Figs. 6–13. Tergum VII of male (postero-dorsal view). 6. *Quartinia australis*, 7. *Quartinia bonaespei*, 8. *Quartinia conchicola*, 9. *Quartinia namaquensis*, 10. *Quartinia obibensis*, 11. *Quartinia refugicola*, 12. *Quartinia vexillata*, 13. *Quartinia femorata*. [TergumVII of *Quartinia namaqua* is very similar to that of *Quartinia obibensis* (Fig. 10)].

dra divaricata; 1 ♂ reared ex *Quartinia* nest in sand-filled *Theba pisana* shell, emerged in lab. 8.viii.2006) [AMG].

Geographic distribution.—Known only from the supra-littoral dunes of the Atlantic seaboard of the Western Cape, from Donkinsbaai, circa 220 km north of Cape Town to Bloubergstrand at the northern extremity of Table Bay (the type locality). At Yzerfontein it has been found together with *Q. namaqua* and *Q. obibensis*.

Floral associations.—Asphodelaceae (*Trachyandra*) and Aizoaceae: Mesembryanthema (including *Conicosia* and *Drosanthemum*).

Nesting.—The collection at all the listed localities of adult females from sand-filled snail shells, the discovery of an adult female at Bloubergstrand in a shell containing also an open cell provisioned with a mixture of pollens including that of *Trachyandra divaricata*, and the rearing in the lab of adults from mature larvae extracted from cells found in shells from four of the localities, demonstrates that this species, like others occurring in sandy areas, utilizes sand-filled snail shells as a nesting niche. Shells of the indigenous desert snail, *Trigonephrus* species (Mollusca: Gasteropoda: Pulmonata: Dorcasii-

dae) are the original ones utilized and appear to be preferred; where these are in short supply, the smaller, thinner and therefore less opaque shells of the exotic *Theba pisana* (Müll.) (Mollusca: Gasteropoda: Pulmonata: Helicidae) are used.

Quartinia conchicola Gess, new species

Quartinia sp. (larger sp.) (Gess and Gess 1999, nesting)

Diagnosis.—Very large (5.6–6.3 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Both sexes with vertex behind posterior ocelli depressed, somewhat concave; with fore coxa not swollen basally nor anteriorly produced but evenly curved. Male with fore femur enlarged, excavated beneath and undulate postero-ventrally; tibia robust, markedly swollen, appreciably shorter than femur and, when opposed to femur, fitting into ventral excavation of same.

Description.—Female: Black. The following are yellowish-white: short (almost medially interrupted) and laterally widening transverse band on dorsum of pronotum and minute spot at postero-dorsal angle of same; humeral streak of varying length; anterior and posterior thirds of tegula (median third clear, testaceous); medially interrupted band on lamellate margin of scutellum (specimens from Hondeklip Bay only). (The specimen from Knersvlakte lacks the humeral streak as do those from between Alexander Bay and Port Nolloth which in addition have the other markings on the thorax reduced and reddish-brown. Those from W of Wallekraal are without thoracic markings.) The following are various shades of light reddish brown: mandible (other than base); labrum; lower aspect of pedicel and flagellum; posterior bands (in some specimens widened medially and usually not attaining lateral margins) on terga I–IV (or V); apices of all femora; most of tibia and tarsus of all legs. Venation light brown at base of wings, otherwise very dark brown. Wing membrane very slightly browned. Length 5.6–6.3 mm (average of 8 = 6.1 mm); length of fore wing 3.7–4.2 mm (average of 8 = 4.1 mm); hamuli 6.

Head in front view 1.3–1.34 × as wide as long; POL:OOL = 1:0.65 (average of 5). Vertex behind posterior ocelli depressed, somewhat concave.

In general facies similar to male (described below) but with legs and last tergum simple.

Male: Head and mesosoma black, gaster and greater part of femora of all legs very dark brown to almost black. The following are yellowish-white: pair of small spots on frons immediately above frontoclypeal suture (in specimens from north of Vanrhynsdorp only); short (almost medially interrupted) and laterally widening transverse band on dorsum of pronotum and minute spot at postero-dorsal angle of same; humeral streak of varying length; anterior and posterior thirds of tegula (median third clear, testaceous); medially interrupted band on lamellate margin of scutellum. (In a specimen from between Alexander Bay and Port Nolloth the humeral markings are absent and the other markings on the thorax are reddish-brown.) The following are various shades of light reddish brown: mandible (other than base); labrum; lower aspect of scape, pedicel and flagellum; posterior bands (slightly widened medially and laterally but not attaining lateral margins) on terga I–VI; apices of all femora; most of fore tibia; middle tibia and hind tibia to variable extent and tarsus of all legs. Venation light brown at base of wings, otherwise very dark brown. Wing membrane very slightly browned.

Length circa 5.8–6 mm; length of fore wing circa 4–4.5 mm.

Head, mesosoma and terga I–VII very finely microsculptured (shagreened) but nevertheless shiny.

Head in front view 1.4–1.45 × as wide as long; POL:OOL = 1:0.65.). Vertex behind posterior ocelli depressed, somewhat concave.

Tegula with posterior inner corner inwardly produced. Wing venation with Cu1 and 2*m-cu* complete and as thick as other veins.

Fore leg with coxa unmodified; femur (Fig. 2) enlarged, excavated beneath and undulate postero-ventrally; tibia robust, markedly swollen, appreciably shorter than femur and when opposed to femur fitting into ventral excavation of same.

Middle and hind femora robust but otherwise not markedly modified.

Sternum I postero-medially very slightly bi-tuberculate; sternum II somewhat raised on either side of median area. Tergum VII (Fig. 8) in posterior half with dorsal surface raised laterally and delimited by low carinae, produced apically and with a deep, narrow, slightly sub-parallel median slit.

Etymology.—The name *conchicola* is a compound word formed from the Latin words *concha – ae* – the shell of a mollusc, and *cola* – a dweller. It serves to draw attention to the species' association, albeit not unique, with sand-filled shells of the Desert Snail, *Trigonephrus*, in which its nests are sheltered from prevailing winds.

Material examined.—Holotype: ♂, SOUTH AFRICA: WESTERN CAPE: 12 km N of Vanrhynsdorp (31.31S 18.43E), 27.ix.2005 (F. W. and S. K. Gess) (dead, ex nest in sand-filled *Trigonephrus* shell) [AMG]. Paratypes: SOUTH AFRICA: NORTHERN CAPE: Richtersveld National Park, 1.5 km from Helskloof Gate (28.18S 16.57E), 8.ix.1996 (F. W., S. K. and R. W. Gess), 1 ♀ (on white flowers of *Pelargonium klinghardtense* Knuth, Geraniaceae) [AMG]; Richtersveld, W of Brandkaros (28.29S 16.40E), 15.ix.1996 (F. W., S. K. and R. W. Gess), 1 ♂ (dead) and fragments of 2 further ♂♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]; between Alexander Bay and turnoff to Oranjemund (28.35S 16.30E) 13.ix.1996 (F. W., S. K. and R. W. Gess), 1 ♀ (dead, ex nest in sand-filled *Trigonephrus* shell) [AMG]; 24 km S of Alexander Bay on road to Port Nolloth [= 60 km N of Port Nolloth on road to Alexander Bay] (28.47S 16.38E), 27.ix.1997 (F. W. and S. K. Gess), 5 ♀♀ (4 ex nests in sand-filled *Trigonephrus* shells; 1 on ground) [AMG]; same locality, 11.x.2000 (F. W. and S. K. Gess), 1 ♀ (visiting pink flowers of *Drosanthemum* sp.) [AMG]; 60 km S of Alexander Bay on road to Port Nolloth (28.51S 16.40E), 19.ix.1996 (F. W., S. K. and R. W. Gess), 1 ♂ (dead, ex nest in sand-filled *Trigonephrus* shell) [AMG]; Hondeklip Bay (30.19S 17.17E), 12.x.1994 (F. W. and S. K. Gess), 3 ♀♀ (visiting yellow flowers of *Conicosia* sp., Aizoaceae: Mesembryanthema) [AMG]; W of Wallekraal (30.21S 17.26E), 8.x.1997 (F. W. and S. K. Gess), 2 ♀♀ (live) and fragments of 1 ♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]. WESTERN CAPE: Knersvlakte, 48 km N of Vanrhynsdorp (31.14S 18.32E), 20.ix.1996 (F. W., S. K. and R. W. Gess), 1 ♀ [AMG]; 12 km N of Vanrhynsdorp (31.31S 18.43E), 27.ix.2005 (F. W. and S. K. Gess), 2 ♀♀, 2 ♂♂ (dead and incomplete, ex nests in sand-filled *Trigonephrus* shells) [AMG]; SE of Lutzville on road to Vredendal (31.36S 18.23E), 29.ix.2005 (F. W. and S. K. Gess), 3♀♀ (reared from mature larvae ex *Quartinia* nests ex sand-filled *Trigonephrus* shells, emerged in lab at the end of April 2007) [AMG].

Geographic distribution.—The species is known from South Africa from the western part of the Northern Cape, mainly along the seaboard from the Orange River southwards, and from the northwestern Western Cape where it extends inland to a distance of about 50 km. In occurs variously together with *Q. namaqua*, *Q. namaquensis*, *Q. obibensis*, *Q. rufigicola* and *Q. vexillata*.

Floral associations.—Aizoaceae: Mesembryanthema (*Conicosia*, *Drosanthemum*), Geraniaceae (*Pelargonium*).

Nesting.—Throughout its presently known distributional area found nesting in sand-filled shells of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda: Pulmonata: Dorcasiidae). For further details see Gess and Gess (1999).

Discussion.—*Q. conchicola* and *Q. vexillata* appear to be closely allied and at least in the north-western Richtersveld (S of Alexander Bay) overlap in their distribution. Whereas the males are readily distinguishable on the basis of secondary sexual characters – notably the differently modified fore legs – the females are deceptively similar and at first sight are very difficult to separate. They may, however, be distin-

guished by characters which they share with their respective males: *Q. conchicola* by the depressed, somewhat concave vertex and by the unmodified fore coxae and *Q. vexillata* by the evenly convex vertex and by the basally swollen and anteriorly produced fore coxae.

Quartinia namaqua Gess, new species

Diagnosis.—Very large (5.8–6.2 mm). Fore wing with Cu1a and *2m-cu* complete and as thick as other veins. Tegula with posterior inner corner markedly inwardly produced, reddish brown. Both sexes with head and thorax black (except, in most specimens, a small reddish-brown marking medially on anterior margin of pronotum); gaster black with a variable number of reddish brown posterior bands which do not attain sides of terga. Parapsidal furrows very noticeable. Male with clypeus evenly convex (not medially depressed), closely and finely sculptured; with sternum I postero-medially raised into a pronounced tubercle; tubercle viewed from behind with widely rounded (almost subtruncate) apex, viewed from the side sloping steeply anteriorly and falling steeply posteriorly to hind margin of sternum. Tergum VII with distinct dorsal and lateral surfaces; apex drawn out into a pair of parallel processes flanking narrow and slit-like emargination; emargination produced anteriorly as a median impression.

Description.—Female: Black. The following are reddish-brown: mandibles distally; underside of pedicel and flagellum; in two of the northern specimens a mere indication of a transverse marking on anterior margin of pronotum; tegula; posterior bands not attaining sides on terga 1–IV (in southern specimens on terga I–III only); that on I of even width and covering about half of tergum; those of terga II and III narrower but medially expanded; that of IV short or (in two specimens) barely indicated; in northern specimens apex of femur, entire or most of tibia, tarsomeres (progressively darkened) of all legs; in two of the southern specimens apex of femur, base and apex of tibia and base of first tarsomere only. Wings slightly darkened; veins brown.

Length 6.2 mm; length of fore wing 3.9 mm; hamuli 6.

Head in front view 1.3 × as wide as long; clypeus 1.1 × as wide as long (length measured to bottom of emargination); POL:OOL = 1:0.9. Clypeus very closely microsculptured, with barely discernable shallow punctures, dull; frons and vertex similarly microsculptured but somewhat more obviously punctured, moderately shiny; mesosoma microsculptured with obvious shallow punctures; interstices of puncture width or less; parapsidal furrows very obvious; gaster finely and closely punctured, shiny.

Male: Black. The following are reddish-brown: mandibles distally; scape apically, pedical, upper and lower side of flagellomeres (except distal part of club); transverse marking on anterior margin of pronotum; tegula; posterior band not attaining sides on tergum I and mere indication of band on tergum II; apex of femur, most of tibia, tarsomeres (progressively darkened) of all legs.

Length 5.8 mm; length of fore wing 3,6 mm; hamuli 6.

Head in front view 1.4 × as wide as long; clypeus 1.1 × as wide as long (length measured to bottom of emargination); POL:OOL = 1:0.8. Clypeus evenly convex, closely microsculptured, with barely discernable shallow punctures, only moderately shiny; frons and vertex similarly microsculptured but somewhat more obviously punctured, moderately shiny; mesosoma microsculptured with obvious shallow punctures; interstices of puncture width or less; parapsidal furrows very obvious; gaster finely and closely punctured, shiny. Sternum I postero-medially raised into a pronounced tubercle; tubercle viewed from behind with widely rounded (almost subtruncate) apex, viewed from

the side sloping steeply anteriorly and falling steeply posteriorly to hind margin of sternum. Tergum VII with distinct dorsal and lateral surfaces; apex drawn out into a pair of parallel processes flanking narrow and slit-like emargination; emargination produced anteriorly as a median impression.

Etymology.—The name, *namaqua*, a noun in apposition to the generic name, is derived from the Namaqua people of Namaqualand and refers to the provenance of the species.

Material examined. – Holotype, ♂, SOUTH AFRICA: NORTHERN CAPE: Inland of Hondeklip Bay (30.19S 17.17E), 25.ix.2005 (F W and S K Gess) (ex nest in sand-filled *Trigonephrus* shell) [AMG]. Paratypes: SOUTH AFRICA: NORTHERN CAPE: same data as holotype, 1 ♀ [AMG]; between Hondeklip Bay and Wallekraal (30.22S 17.28E), 25.ix.2005 (F W and S K Gess), 1 ♀ (ex nest in sand-filled *Trigonephrus* shell) [AMG]. WESTERN CAPE: SE of Lutzville on road to Vredendal (31.36S 18.23E), 29.ix.2005 (F W Gess and S K Gess), 1 ♀ (visiting yellow flowers of *Conicosia* sp., Aizoaceae: Mesembryanthema) [AMG]; Yzerfontein (33.20S 18.10E), 15.x.2006 (D. W., G. T. and G. M. Gess), 3 ♀♀ (ex *Theba pisana* shells) [AMG].

Geographic distribution.—The species is known from South Africa from the southwestern Northern Cape, from the northwestern Western Cape, and from Yzerfontein in the southwestern Western Cape, and therefore will probably be found to occur all along the coastal sandveld between the above areas. In occurs variously together with *Q. bonaespei*, *conchicola*, *namaquensis* and *obibensis*.

Floral associations.—Aizoaceae: Mesembryanthema (*Conicosia*).

Nesting.—At two localities found nesting in sand-filled shells of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda: Pulmonata: Dorcasiidae) and at another obtained from shells of the exotic *Theba pisana* (Müll.) (Mollusca: Gasteropoda: Pulmonata: Helicidae).

Discussion.—*Q. namaqua* is superficially very similar to *Q. obibensis*, most notably in the male in the possession of a raised tubercle postero-medially on sternum I. It may be distinguished in both sexes by the more distinct and somewhat less close puncturation of the mesoscutum and scutellum, by the broader and much more noticeable parapsidal furrows, and by the interocellar distance only slightly exceeding the ocellar-ocular distance [POL:OOL = 1:0.9 (♀) and 1:0.8 (♂) as against 1:0.7 (both sexes)]. The male may be distinguished by the evenly convex, closely microsculptured and only moderately shiny clypeus in contrast to the medially depressed, non-microsculptured but sparsely punctured and shiny clypeus of *Q. obibensis*. In colour pattern the species differs in that the reddish-brown markings are reduced, most notably in that the posterior bands on the gaster do not attain the lateral margins of the terga.

Quartinia namaquensis Gess, new species

Diagnosis.—Very large (5.8–6.0 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula short, laterally rounded, with posterior inner corner inwardly produced. Male black with white-marked labrum, clypeus, frons, pronotum, tegula, scutellar lamella, and terga I–VI. Fore leg greatly enlarged and modified; middle and hind legs somewhat modified. Tergum VII drawn out apicomedially into a robust, pointed, dorsally flattened and apically narrowly rounded process.

Description.—Male: Black. The following are white: labrum; disc of clypeus; paraocular streak from mandibular insertion to level of top of antennal socket (specimen from Wallekraal only); supra-clypeal marking (more or less quadrate and bilobed dorsally in specimens from Leliefontein but in specimen from Wallekraal expanded on each side with lobe directed laterally towards ocular sinus and another directed dorsally); underside of scape, pedical and proximal flagellomeres; continuous anteri-

or band on pronotum (narrowly and pointedly extended a little along dorso-lateral margin and broadly continuous onto humerus and beyond) and minute spot on postero-dorsal angle of same; small spot at top of mesopleuron (specimen from Wallekraal only); tegula (except for median testaceaous area); scutellar lamella (other than medially); lower two thirds of metanotum (specimen from Wallekraal only); minute dots dorsally on propodeum (one specimen from Leliefontain only) or small streak unilaterally on angle of propodeum (specimen from Wallekraal only); narrow posterior bands, almost reaching sides, on terga I–VI. The following are light reddish yellow: mandible (except base and apex): labrum (if not white); posterior bands, slightly medially expanded, on sterna; underside of trochanter of all legs; entire anterior surface of fore femur as well as posterior surface of basal lamelliform angle of same; underside of basal half of mid femur (most specimens); apices of femora and entire tibiae, tarsi and claws of all legs. Wing membrane sub-hyaline; veins brown.

Length 5.8–6.0 mm.; length of fore wing 3.8–3.9 mm.; hamuli circa 6.

Head in front view 1.33 × as wide as long, microreticulate, moderately shiny, with shallow punctures (small and close on frons, slightly larger and more widely spaced on vertex). POL:OOL = 1:0.59. Clypeus 1.5 × as wide as long in midline; anterior margin widely and shallowly emarginate.

Mesosoma microreticulate, moderately shiny, with punctures larger than those on head (moderately well separated on pronotum, mesoscutum and scutellum).

Tegula short, laterally rounded, with posterior inner corner inwardly produced.

Fore leg much modified; coxa and trochanter enlarged; femur (Fig. 3) greatly swollen, its posterior surface in proximal half markedly concavely excavate, smooth and very shiny, its baso-ventral region angulate and sublamellate; first tarsomere swollen, excavate and setose below; second tarsomere in posterior view curved, wide at base but otherwise narrow, with long , backwardly curved setae; middle and hind legs beneath with trochanters flattened and with femora angulate, flattened in proximal half and longitudinally grooved in distal half.

Metasoma moderately shiny, with punctures finer than those on head. Tergum VII (Fig. 9) drawn out apico-medially into a robust, pointed, dorsally flattened and apically narrowly rounded process.

Female: Unknown, none of the specimens of several species from the relevant localities being assignable with any degree of confidence to this species.

Etymology.—The name, *namaquensis*, an adjective, is derived from the Namaqua people of Namaqualand and refers to the provenance of the species.

Material examined.—Holotype, ♂, SOUTH AFRICA: NORTHERN CAPE: Leliefontein (30.23S 18.16E), 31.vii.2003 (C. Mayer), 1 ♂ (yellow trap) [AMG]. Paratypes: SOUTH AFRICA: NORTHERN CAPE: same data as holotype but date 15.ix.2003, 1 ♂ [AMG]; same data as holotype but date 22.viii.2004, and trap white, 1 ♂ [AMG]; W of Wallekraal (30.21S 17.26E), 8.x.1997 (F. W. and S. K. Gess), 1 ♂ (ex nest in sand-filled *Trigonephrus* shell) [AMG].

Geographic distribution.—Known only from two localities in Namaqualand, one in the coastal sandveld, the other in the Kamiesberg. In the former locality it occurs together with *Q. conchicola* and *Q. namaqua*.

Floral associations.—Unknown.

Nesting.—One specimen, freshly eclosed and with wings not yet fully hardened, was extracted from a cell of a nest in a sand-filled shell of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda: Pulmonata: Dorcasiidae).

Quartinia obibensis Gess, new species

Diagnosis.—Large to very large (5.2–5.7 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as the other veins. Tegula with posterior inner corner markedly inwardly produced, reddish brown. Both

sexes with head and thorax predominantly black with limited reddish-brown markings; gaster black with well developed reddish-brown posterior bands attaining or almost attaining side of terga. Male with clypeus medially depressed, sparsely punctured and shiny; with sternum I postero-medially raised into a small tubercle; tubercle viewed from behind transversely subtriangular with a narrowly rounded apex, viewed from the side sloping gradually anteriorly and falling steeply posteriorly to hind margin of sternum. Tergum VII with distinct dorsal and lateral surfaces; apex drawn out into a pair of parallel processes flanking narrow and slit-like emargination; emargination produced anteriorly as a median impression.

Description.—Female: Black. The following are reddish-brown: mandibles (except base); underside of pedicel and flagellomeres; anterior margin of pronotum and postero-dorsal angle of same; tegula; crescent (in some specimens broken up into spots) posteriorly and laterally on disk of scutellum; scutellar lamella; in some specimens lower half of metanotum; posterior bands attaining or almost attaining sides on terga I–V; that on I of even width and covering about half of tergum; those of terga II–V progressively narrower, undulate, expanded medially and laterally and attaining or almost attaining sides of terga); apical spot on tergum IV; apex of femur, entire tibia, tarsomeres (except last) of all legs. Last tarsomere and claws brown. Wings slightly darkened; veins brown.

Length 5.2–5.7 mm (average of 4:5.4 mm); length of fore wing 3.6–3.7 mm (average of 4:3.7 mm); hamuli 5.

Head in front view 1.35 × as wide as long, microreticulate, matt, with inconspicuous, very shallow, fine punctures. POL:OOL = 1:0.7. Clypeus 1.33 × as wide as long (length measured to bottom of emargination; 1.2 × if measured to level of antero-lateral angles); anterior margin smooth, shiny, shallowly and evenly emarginate.

Mesosoma microreticulate with close, shallow, fine punctures, slightly shiny. Gaster finely microreticulate but shiny; punctures finer than those on mesosoma, becoming progressively finer distally.

Tegula with posterior inner corner markedly inwardly produced.

Male: Black. The reddish-brown markings as in the female, with in addition: labrum (to varying degree); in some specimens small antero-lateral spots (occasionally joined) on clypeus.

Length 5.2 mm; length of fore wing 3.5 mm.

POL:OOL = 1:0.7

Clypeus medially depressed, non-microsculptured but sparsely punctured and shiny. Sternum I postero-medially raised into a small tubercle; tubercle, viewed from behind, transversely subtriangular with a narrowly rounded apex, anteriorly gradually sloping, posteriorly falling steeply to hind margin of sternum. Tergum VII (Fig. 10) with distinct dorsal and lateral surfaces; apex drawn out into a pair of parallel processes flanking narrow and slit-like emargination; emargination produced anteriorly as a median impression.

Etymology.—The name, *obibensis*, an adjective, is derived from the Obib Mountains in the Sperrgebiet of south-western Namibia, the site from which the largest number of specimens was obtained.

Material examined.—Holotype: ♂, NAMIBIA: Sperrgebiet, Obib camp site (28.00S 16.39E), 14.ix.2003 (F. W. and S. K. Gess) (ex nest in sand-filled *Trigonephrus* shell, emerged in the lab. 15–22.x.2003) [AMG]. Paratypes: NAMIBIA: Sperrgebiet, W of Klinghardtberge (27.17S 15.36E), 20.ix.2003 (F. W. and S. K. Gess), 4 ♀♀ (ex nests in sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Klinghardtberge (27.19S 15.46E), 10.ix.2005 (F. W. and S. K. Gess), 1 ♀ (reared ex *Quartinia* nest in sand-filled *Trigonephrus* shell) [AMG]; Sperrgebiet, Klinghardtberge (27.30S, 15.44E), 10.ix.2005 (F. W. and S. K. Gess), 1 ♀, 1♂ (reared ex *Quartinia* nests in sand-filled *Trigonephrus* shells) [AMG]; Aus – Rosh Pinah (27.44S 16.42E), 25.ix.2003 (F. W. and S. K. Gess), 1 ♂ (visiting white centered, purplish-pink rayed *Drosanthemum* sp., Aizoaceae: Mesembrianthema) [AMG;]; Sperrgebiet,

between Aurusberg and Scorpion Mine (27.45S 16.32E), 15.ix.2003 (F. W. and S. K. Gess), 1 ♀, 2 ♂♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Scorpion Mine (27.49S 16.35E), 15.ix.2003 (F. W. and S,. K. Gess), 4 ♀♀, 1 ♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Obib camp site (28.00S 16.39E), 14.ix.2003 (F. W. and S. K. Gess), 37 ♀♀, 13 ♂♂ (ex nests in sand-filled *Trigonephrus* shells; 26 ♀♀, 2 ♂♂ emerged in the lab. 15–22.x.2003; 7 ♀♀, 2 ♂♂ emerged in lab. at a later date) [AMG]; 12.8 km S Rosh Pinah (28.03S 16.51E) 11.ix.1996 (F. W., S. K. and R. W. Gess), 3 ♀♀, 3 ♂♂ (ex nests in sand-filled *Trigonephrus* shells; 2 ♀♀, 3 ♂♂ emerged in lab.) [AMG]. SOUTH AFRICA: NORTHERN CAPE: Richtersveld, W of Brandkaros (28.29S 16.40 E), 15.ix.1996 (F. W., S. K. and R. W. Gess), 3 ♀♀, 1 ♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]. WESTERN CAPE: Yzerfontein (33.20S 18.10E), 15.x.2006 (D. W., G. T. and G. M. Gess), 2 ♂♂ (ex *Theba pisana* shells) [AMG].

Geographic distribution.—*Q. obibensis* is known from Namibia, from a limited area in the southern half of the Desert and Succulent Steppe (Winter Rainfall Area) of Giess (1971), from South Africa from a nearby locality in the Richtersveld and from a coastal site in the Western Cape. In the north of its range it occurs together with *Q. conchicola*, *Q. rufigicola* and *Q. vexillata* and in the south with *Q. bonaespei and Q. namaqua*.

Floral associations.—Aizoaceae: Mesembryanthema (*Drosanthemum*).

Nesting.—Throughout its presently known distributional area found nesting most commonly in sand-filled shells of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda: Pulmonata: Dorcasiidae). At one coastal locality in the Western Cape obtained from shells of the exotic *Theba pisana* (Müll.) (Mollusca: Gasteropoda: Pulmonata: Helicidae). For further details see Gess and Gess (1999).

Discussion.—See under *Q. namaqua*.

Quartinia refugicola Gess, new species

Quartinia sp. (smaller sp.) (Gess and Gess 1999, nesting; Greathead 1999, 2006, bombyliid parasite).

Diagnosis.—Medium sized to large (4.1–5.2 mm long). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula with posterior inner corner inwardly produced. Posterior bands on terga reaching lateral margins.

Description.—*Female*: Black. The following are yellow or yellow merging into brownish yellow: underside of flagellomeres; short, narrow, transverse band (in some specimens reduced to pair of small marks, in others totally absent) medially on pronotum and in some specimens a minute dot on postero-dorsal angle of same; tegula (except for testaceous medial spot); narrow, medially interrupted, lamellate margin of scutellum; in some specimens median part of metanotum; narrow posterior bands reaching lateral margins on terga I–V (that of tergum I widest, others progressively narrower); in some specimens a diffuse posterior band on sternum II; extreme apex of femur, entire tibia (except for elongate dark mark on posterior surface) and tarsomeres of all legs (except in some specimens brown terminal tarsomeres of middle and hind legs). Mandible with distal half bright ferruginous; labrum brown. Wings subhyaline; veins brown.

Length 4.5–5.2 mm (average of 5:4.8 mm); length of fore wing 3.0–3.4 mm (average of 5:3.2 mm); hamuli 5–6.

Head in front view 1.3 × as wide as long; clypeus 1.5 × as wide as long (length measured to bottom of emargination); POL:OOL = 1:0.6. Clypeus very closely microsculptured, with barely discernable shallow punctures; frons and vertex similarly microsculptured but more obviously punctured (especially in region of ocelli); mesosoma microsculptured with obvious shallow punctures slightly larger than those on vertex and with interstices of puncture width or less; gaster closely and finely punctured.

Male: Black. Pale markings as in female but with the addition of: in **some** specimens sub-basal spot on mandible between

black base and ferruginous distal half; in **some** specimens part of the clypeus (ranging in extent from pair of anterolateral spots, to uninterrupted anterior margin, to most of disc with exception of region below antennal sockets); in **all** specimens narrow posterior band on tergum VI and in **most** specimens apices of tergum VII.

Length 4.1–4.3 mm (average of 5:4.2 mm); length of fore wing 2.8–2.9 mm (average of 5:2.8 mm); hamuli 4.

Head in front view 1.37 × as wide as long; clypeus convex, 1.5 × as wide as long; POL:OOL = 1:0.6. Microsculpture and puncturation as in female. Tergum VII (Fig. 11) dorsally slightly depressed (flattened) and its apical margin with a narrow V-shaped median emargination flanked by narrowly rounded projections.

Etymology.—The name *refugicola* is a compound word formed from the Latin words *refugium – ii* (n) – a place of refuge, and *cola* – a dweller. It serves to draw attention to the species' association with sand-filled cavities in which its nests are sheltered from prevailing winds.

Material examined.—Holotype: ♂, NAMIBIA: 12.8 km S of Rosh Pinah (28.03 S 16.51E), 11.ix.1996 (F. W., S. K. and R. W. Gess) (on ground) [AMG]. Paratypes: NAMIBIA: Aus (26.39S 16.15E), 25.viii.2002 (F. W. and S. K. Gess), 1 ♀ (visiting yellow flowers of *Leysera tenella* DC., Asteraceae) [AMG]; Sperrgebiet, Kaukausib Spring – Grillental (26.58S 15.31E), 5.ix.2002 (F. W. and S. K. Gess), 4 ♀♀ (visiting white flowers of *Zygophyllum clavatum* Schltr. & Diels, Zygophyllaceae) [AMG]; Sperrgebiet, near Grillental (26.59S 15.23E), 5.ix.2002 (F. W. and S. K.Gess), 1 ♂ (visiting yellow flowers of *Foveolina albida* (DC.) Källersjö, Asteraceae) [AMG]; Sperrgebiet, Grillental (27.00S 15.21E), 8.ix.2005 (F. W. and S. K. Gess), 3 ♀♀, 1 ♂ (visiting white flowers of *Zygophyllum* sp.) [AMG]; Sperrgebiet, Klinghardtberge, Tsabiams Camp (27.10 S 15.42E), 4.ix.2002 (F. W. and S. K. Gess), 1 ♀ (visiting yellow flowers of *Dimorphotheca polyptera* DC., Asteraceae) [AMG]; Sperrgebiet, Klinghardtberge (27.14S 15.43E), 1–3.ix.2002 (F. W. and S. K. Gess), 5 ♀♀ (1 ♀ visiting flowers of ? *Cotula* sp., Asteraceae; 1 ♀ visiting yellow flowers of *Pteronia* sp., Asteraceae; 3 ♀♀ visiting yellow flowers of *Zygophyllum simplex* L., Zygophyllaceae) [AMG]; Sperrgebiet, Klinghardtberge (27.14S 15.44E), 2.ix.2002 (F. W. and S. K. Gess), 6 ♀♀, 1 ♂ (3 ♀♀ visiting yellow flowers of *Pteronia* sp., Asteraceae; 3 ♀♀ visiting apricot coloured flowers of *Phyllobolus occulatus* (N.E.Br.) Gerbaulet, Aizoaceae: Mesembryanthema; 1 ♂ visiting pink flowers of *Sarcocaulon* sp., Geraniaceae) [AMG]; Sperrgebiet, W of Klinghardtberge (27.17S 15.36E), 20.ix.2003 (F. W. and S. K. Gess), 5 ♀♀, 3 ♂♂ (ex nests in sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Klinghardtberge (27.18S 15.54E), 2.ix.2002) (F. W. and S. K. Gess), 1 ♂ [AMG]; Sperrgebiet, Klinghardtberge (27.19S 15.46E), 10.ix.2005 (F. W. and S. K. Gess), 2 ♀♀, 1 ♂ (reared from larvae ex *Quartinia* nests ex sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Klinghardtberge, Nomitsas (27.27S 15.52E), 31.viii.2002 (F. W. and S. K. Gess), 1 ♀, 1 ♂ (ex sand-filled *Trigonephrus* shells) [AMG]; Sperrgebiet, Uguchab River, NW of Aurus Mountains (27.31S 16.12E), 17.ix.2003 (F. W. and S. K. Gess), 31 ♀♀, 20 ♂♂ (17 ♀♀, 10 ♂♂ ex sand-filled *Trigonephrus* shells; 14 ♀♀, 10 ♂♂ ex nests in sand-filled *Trigonephrus* shells) [AMG]; 12.8 km S of Rosh Pinah (28.03 S 16.51E), 11.ix.1996 (F. W., S. K. and R. W. Gess), 29 ♀♀, 32 ♂♂ (21 ♀♀, 26 ♂♂ on ground; 1 ♀ visiting yellow flowers of *Cotula* sp., Asteraceae; 1 ♀ on blue rayed *Filicia* sp., Asteraceae; 1 ♀, 1 ♂ visiting yellow flowers of *Hirpicium* sp., Asteraceae; 1 ♀, 1 ♂ visiting yellow flowers of *Osteospermum* sp., Asteraceae; 1 ♀ visiting yellow flowers of *Grielum* sp., Neuradaceae; 3 ♀♀, 4 ♂♂ ex nests in sand-filled *Trigonephrus* shells; 2 ♂♂ ex sand-filled cavities in calcrete) [AMG]; Sperrgebiet, W of Obib Mountains (28.08S 16.42E), 15.ix.2003 (F. W. and S. K. Gess), 1 ♀ (ex nest in sand-filled *Trigonephrus* shell) [AMG]; E of Oranjemund, 28 km from checkpoint on road to Sendelingsdrif (28.26S 16.42E), 25.ix.1997 (F. W. and S. K. Gess), 1♂ (ex nest in sand-filled *Trigonephrus* shell) [AMG]; E of Oranjemund (28.30S 16.36E), 22.ix.1997 (F. W. and S. K. Gess), 1 ♂ (ex nest in sand-filled *Trigonephrus* shell) [AMG]. SOUTH AFRICA: NORTHERN CAPE: W of Brandkaros (28.29S 16.40E), 13–15.ix.1996 (F. W., S. K. and R. W. Gess), 4 ♀♀ (1 dead), 1 ♂ (dead) (ex nests in sand-filled *Trigonephrus* shells) [AMG]; 60 km N of Port Nolloth (28.47S 16.38E), 27.ix.1997 (F. W.

and S. K. Gess), 1 ♂ (ex nest in sand-filled *Trigonephrus* shell) [AMG].

Geographic distribution.—*Quartinia refugicola* is known from Namibia, from numerous localities in the Desert and Succulent Steppe (Winter Rainfall Region) of Giess (1971) and from the immediately adjacent area across the Orange River in the Northern Cape of South Africa. It occurs together with *Q. conchicola*, *Q. obibensis* and *Q. vexillata*.

Floral associations.—Known in association with Aizoaceae: Mesembryanthema (*Phyllobolus*), Asteraceae (*Cotula*, *Dimorphotheca*, *Filicia*, *Foveolina*, *Hirpicium*, *Leysera*, *Osteospermum* and *Pteronia*), Geraniaceae (*Sarcocaulon*), Neuradaceae (*Grielum*) and Zygophyllaceae (*Zygophyllum*).

Nesting.—Throughout its presently known distributional area most commonly found nesting in sand-filled shells of the desert snail *Trigonephrus* sp. (Mollusca: Gasteropoda: Pulmonata: Dorcasiidae), less commonly in sand-filled cavities in calcrete rocks. See also Gess and Gess (1999). At several localities in the Sperrgebiet nests have been found to be parasitised by *Apolysis hesseana* Evenhuis and Greathead (Bombyliidae: Usiinae: Apolysini). See also Greathead (1999:155; 2006: 5).

Quartinia vexillata Gess, new species

Diagnosis.—Large to very large (5.2–6.5 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Both sexes with vertex behind posterior ocelli evenly convex; with fore coxa swollen basally and anteriorly produced, very markedly so in male, less so in female where swelling, however, forms a rounded right angle. Male with fore femur greatly enlarged, robust, proximally produced ventrally to form a sturdy, subquadrate flange, distally markedly downcurved; flange with its posteriorly facing surface markedly concave with pronounced distal angles and its anteriorly facing surface convex with a pronounced submedian distal tubercle; tibia robust with dense setae on lower surface.

Description.—*Female*: In general facies similar to male (described below) but with legs and last tergum simple. Head without any pale markings. Specimens from between Alexander Bay and Port Nolloth have the mesosoma and gaster with both yellowish white and reddish brown markings very similar to those of males from the same population; specimens from SSE of Grillental and from Obib have the markings on the mesosoma tending to reddish brown. Microsculpture (shagreening) of head and mesosoma somewhat coarser and these parts, in particular mesoscutum, semi-matt rather than shiny.

Length 5.8–6.5 mm (average of 7 = 6.1 mm); length of fore wing 3.9–4.4 mm (average of 7 = 4.1 mm); hamuli 6.

Head broad, 1.33 × as wide as long; POL:OOL = 1:0.5. Vertex behind posterior ocelli evenly convex. Fore coxa enlarged, basally markedly and roundly anteriorly produced.

Male: Head and mesosoma black, gaster and greater part of femur of all legs very dark brown to almost black. The following are yellowish white: lower aspect of scape (excluding radicle) and pedicel; labrum (in one specimen testaceous); clypeus (other than for irregular area below antennal socket); a small transverse spot situated on either side of midline of frons immediately above frontoclypeal suture (in one specimen only); narrow paraocular streak from mandibular insertion to level of top of antennal socket; short (in one specimen almost medially interrupted) and laterally widening transverse band on dorsum of pronotum and minute spot at posterodorsal angle of same; humeral streak of varying length; anterior and posterior thirds of tegula (median third clear, testaceous); medially interrupted band on lamellate margin of scutellum; distal portion of flange on fore femur. The following are various shades of light reddish-brown: mandible (other than base); flagellomeres (other than for dark suffusion on upper

surface); posterior bands (slightly widened medially, narrowed laterally, and not quite attaining lateral margins of terga) on terga I–VI; streak on anteriorly protruding portion of fore coxa (in one specimen) and lower surface of middle and hind coxae; all trochanters; distal portion (up to almost half the length) of anterior aspect of fore femur; basal flattened lower surface of middle femur; apex of middle and hind femora; tibia and tarsus of all legs. Venation light brown at base of wings, otherwise very dark brown. Wing membrane very slightly browned, a little darker on fore wing in and beyond marginal cell.

Length 5.2–6.4 mm; length of fore wing 3.6–3.8 mm; hamuli 6.

Head, mesosoma and terga I–VI very finely microsculptured (shagreened) but nevertheless shiny, with moderately sized punctures; punctures on head and terga somewhat shallow and undefined with interspaces generally less than puncture diameter, those on mesosoma deeper and well defined with interspaces at least on mesoscutum often greater than puncture diameter. Tergum VII without microsculpture; punctures more pronounced than those on other terga, irregularly spaced, some separated by wide interspaces and others coalescing.

Setation on head and particularly on body sparse and short throughout, more noticeable on tibiae and tarsi and strikingly developed on underside of front tibia where dense and long.

Head broad, 1.45 × as wide as long; POL:OOL = 1:0.5. Vertex behind posterior ocelli evenly convex;

Tegula with posterior inner corner inwardly produced. Wing venation with Cu1a and 2*m-cu* complete and as thick as other veins.

Fore leg uniquely and greatly modified; coxa enlarged, basally markedly and roundly anteriorly produced; femur (Fig. 4) greatly enlarged, robust, proximally produced ventrally to form a sturdy, subquadrate flange, distally markedly downcurved; flange with its posteriorly facing surface markedly concave with pronounced distal angles and its anteriorly facing surface convex with a pronounced submedian distal tubercle; tibia robust with dense setae on lower surface.

Middle and hind femora robust, markedly angled below and with lower surface both proximal and distal to angle distinctly flattened (more so on middle than on hind femur).

Tergum VII (Fig. 12) in posterior half with dorsal surface raised laterally and slightly concave medially, produced apically and with a deep, narrow, slightly subparallel-sided median slit.

Etymology.—The name *vexillata* is formed from the Latin noun *vexillum* meaning a flag or standard. It refers to the conspicuously modified front femur of the male which may possibly have a communicatory role in courtship behaviour.

Material examined.—Holotype: ♂, SOUTH AFRICA: NORTHERN CAPE: 23 km S of Alexander Bay (28.46S 16.37E), 11.x. 2000 (F. W and S. K. Gess) (on ground) [AMG]. Paratypes: NAMIBIA: Sperrgebiet, main north/south road, 47 km SSE of Grillental (27.23S 15.32E), 6.ix.2002 (F. W. and S. K. Gess), 2 ♀♀ (on ground next to *Drosanthemum* sp., Aizoaceae: Mesembryanthema) [AMG]; Sperrgebiet, Obib camp site (28.00S 16.39E), 14.ix.2003 (F. W. and S. K. Gess), 9 ♀♀ (7 ♀♀ visiting yellow flowers of *Cephalophyllum* sp., Aizoaceae: Mesembryanthema; 2 ♀♀ visiting yellow flowers of *Othonna cylindrica* (Lam.) DC., Asteraceae) [AMG]. SOUTH AFRICA: NORTHERN CAPE: 23 km S of Alexander Bay (28.46S 16.37E), 11.x. 2000 (F. W and S. K. Gess), 5 ♀♀ (4 ♀♀ visiting pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembryanthema; 1 ♀ visiting purple-centred white flowers, Aizoaceae: Mesembryanthema) [AMG]; 60 km N of Port Nolloth (28.47S 16.38E), 27. ix. 1997) F. W. and S. K. Gess), 6 ♀♀, 1 ♂ (2 ♀♀, ♂ visiting pale pink flowers of *Drosanthemum* sp.; 4 ♀♀ on ground) [AMG].

Geographic distribution.—The species is known from Namibia from the Desert

and Succulent Steppe (Winter rainfall area) of Giess (1971) and from South Africa from the adjoining northern Strandveld of the West Coast of Acocks (1953). It occurs variously together with *Q. conchicola*, *Q. obibensis* and *Q. refugicola*.

Floral associations.—Aizoaceae: Mesembryanthema (*Cephalophyllum*, *Drosanthemum*); Asteraceae (*Othonna*).

Nesting.—Unknown; probably utilizing sand-filled snail shells as a nesting niche.

Discussion.—See under *Q. conchicola*.

KEY TO SPECIES NESTING IN SAND-FILLED SNAIL SHELLS OR (*VEXILLATA*) PRESUMED TO DO SO

Males

1. Fore legs not modified 2
- Fore legs markedly modified 5
2. Sternum I not modified 3
- Sternum I posteriorly raised into a tubercle 4
3. Large (5.0–5.4 mm long); black with white markings; tegula with white anterior and posterior markings contrasting markedly with dark brown to black median part; pale posterior bands on terga not extending onto sides; clypeus and labrum white ..... ***australis*** Gess n. sp.
- Medium (4.1–4.3 mm long); black with yellow to brownish-yellow markings; tegula with pale anterior and posterior markings not contrasting markedly with testaceous median part; pale posterior bands on terga reaching lateral margins ..... ***refugicola*** Gess n. sp.
4. Clypeus convex ..... ***namaqua*** Gess n. sp.
- Clypeus depressed to concave ..... ***obibensis*** Gess n. sp.
5. Posterior bands on terga white; not contrasting in colour with markings on head and mesosoma; fore femur (Fig. 3) greatly swollen, its posterior surface in proximal half markedly concavely excavate, smooth and very shiny, its baso-ventral region angulate and sublamellate ..... ***namaquensis*** Gess n. sp.
- Posterior bands on terga reddish-brown or bright reddish-orange, in most specimens contrasting in colour with markings on head and mesosoma; fore femur differently formed 6
6. Tibiae and tarsi of all legs predominantly black; fore femur (Fig. 1) greatly swollen, postero-basally with a pointed tubercle, its posterior surface depressed, smooth and very shiny and forming an angle with ventral surface ..... ***bonaespei*** Gess sp. n.
- Tibiae and tarsi of all legs predominantly light reddish-brown 7
7. Vertex behind posterior ocelli evenly convex; fore coxa swollen basally and markedly anteriorly produced; fore femur (Fig. 4) greatly enlarged, robust, proximally produced ventrally to form a sturdy subquadrate flange, distally markedly downcurved; flange with its posterior facing surface markedly concave with pronounced distal angles and its anterior facing surface convex with a pronounced submedian distal tubercle ..... ***vexillata*** Gess n. sp.
- Vertex behind posterior ocelli depressed, somewhat concave; fore coxae unmodified; fore femur (Fig. 2) enlarged, excavated beneath and undulate postero-ventrally ..... ***conchicola*** Gess n. sp.

Females

Species not included: *namaquensis* Gess n. sp. (♀ not known)

1. Markings on mesosoma and gaster generally concolorous 2

- Markings on mesosoma and gaster not of same colour; posterior bands on terga reddish-brown or bright reddish-orange, generally contrasting with pale markings on mesosoma 5
2. Black with white markings; tegula with anterior and posterior markings contrasting markedly with dark brown to black median part; posterior bands on terga not extending onto sides ..... ***australis*** Gess sp. n.
- Black with yellow, brownish-yellow or reddish-brown markings; tegula with anterior and posterior markings not contrasting markedly with median part; posterior bands on terga variously developed 3
3. Posterior bands on terga reaching lateral margins; scutellar disk black and scutellar lamella yellow to brownish yellow ..... ***refugicola*** Gess sp.n.
- Without this combination of characters 4
4. Mesoscutum and scutellum with interstices between punctures not obviously microreticulate (shagreened); scutellar disk and scutellar lamella black; scutellar lamella at most slightly flattened postero-medially; metanotum not transversly impressed, black throughout ..... ***namaqua*** Gess n. sp.
- Mesoscutum and scutellum with interstices between punctures very obviously microreticulate (shagreened); scutellar disk laterally and medially with reddish-brown markings and scutellar lamella of same colour; scutellar lamella slightly emarginate postero-medially; metanotum transversely impressed with lower section reddish brown and contrasting with almost black upper section ..... ***obibensis*** Gess n. sp.
5. Tibiae and tarsi of all legs predominantly black ..... ***bonaespei*** Gess sp. n.
- Tibiae and tarsi of all legs predominantly light reddish-brown 6
6. Vertex behind posterior ocelli evenly convex; fore coxae swollen basally and markedly anteriorly produced ..... ***vexillata*** Gess n. sp.
- Vertex behind posterior ocelli depressed, somewhat concave; fore coxae unmodified ..... ***conchicola*** Gess n. sp.

B) Other species

Quartinia femorata Gess, new species

Diagnosis.—Very large to gigantic (5.8–6.7 mm long). Fore wing with Cu1a and 2*m-cu* complete and as thick as the other veins. Tegula with posterior inner corner inwardly produced. Both sexes predominantly yellow. Male fore femur robust, notched ventrally in basal third and with a distally directed, apically rounded, lamellate process.

Description.—Female: Predominantly yellow. Black greatly reduced leaving only: occiput; irregular median band on vertex (posteriorly wide along occipital carina but anteriorly narrowed and closely encompassing ocelli) and on frons (on upper half of similar width to part encompassing ocelli but on lower half trifid with middle arm and outcurved lateral arms reaching clypeal suture and antennal sockets respectively); propleuron (in greater part) and prosternum; median and parapsidal bands on mesoscutum (median band wide at anterior margin, narrowing posteriorly; parapsidal bands not reaching anterior margin and of even width throughout); small antero-median mark on scutellum; anterior half of propodeal dorsum and small spot on each side at bottom of propodeal declivity; transverse marking (either continuous or broken up into three) on declivity of tergum I; abbreviated anterior transverse bands (only visible if metasoma is downwardly flexed) on terga II and III. The following are various shades of light reddish-brown: mandibular teeth; antennal club (apex of last flagellomere dark brown); last one or two tarsomeres

(arolia dark brown); usually concealed anterior third of terga II–VI and poorly defined laterally abbreviated and medially interrupted pre-apical transverse bands on terga II–V. Tegulae yellowish-white except for unpigmented translucent central area and outer margin. Wing membrane hyaline; costa, subcosta, media, thickening at junction of Rs & M, parastigma and stigma light brown, rest of venation contrastingly dark brown.

Length 5.8–6.7 mm (average of 6:6.3 mm; length of front wing 3.8–4.3 mm (average of 6:4.1 mm); hamuli 7.

Head, thorax and gaster sparsely covered with short, semi-erect pale pilosity, slightly longer and most noticeable on head, declivity of propodeum, declivity of tergum I, and sternum VI.

Head in front view 1.25 × as wide as long, microreticulate, with close, fine, shallow punctures on vertex. POL:OOL = 1:0.6. Clypeus 1.2 × as wide as long. Mandible simple, apically strongly bidentate.

Thorax microreticulate; mesoscutum and scutellum with only scattered, inconspicuous, very shallow, small punctures; pronotum and mesopleuron with conspicuous, moderate-sized, shallow punctures. Tegula 1.5 × as long as wide, the posterior inner corner distinctly inwardly produced. Propodeal angles evenly rounded.

Gaster microreticulate and with fine punctures.

Male: Coloration as in female. Parameres light reddish-brown.

Length 5.9–6.3 mm; length of fore wing 3.6–4.3; hamuli 7.

Structurally similar to female but differing in the following respects: fore femur (Fig. 5) considerably more robust, notched ventrally in basal third and with distally directed, apically rounded, lamellate process; tergum VII (Fig. 13) with surface flattened medially, with hind margin widely rounded and medially deeply and narrowly emarginate; sternum VII with surface convex medially, concave laterally, with apical margin widely trilobed, lateral lobes ventrally curved. Genitalia very large (1.5 mm long; i.e. half the length of the gaster); outer ramus of parameres broad in dorsal view, apically obliquely truncate and densely covered with fine, long setae; inner ramus proximally of varying width and distally progressively narrowing and markedly and evenly downcurved to form a sharp, well sclerotized hook attaining level of lateral posterior angle of outer ramus.

Etymology.—The name *femorata* serves to draw attention to the uniquely modified front femur of the male.

Material examined.—Holotype: ♂, NAMIBIA: 11 km S of Swakopmund on inland side of road B2 to Walvis Bay (22.46S 14.32E), 7.iv.2002 (F. W. and S. K. Gess) [AMG]. Paratypes: NAMIBIA: same data as holotype, 6 ♀♀, 13 ♂♂ [AMG]; same data as holotype but date 14.iv.2002, 1 ♀, 2 ♂♂ [AMG]; same data as holotype but date 20.iv.2002, 1 ♀, 4 ♂♂ [AMG]; same data as holotype but date 30.iii.2004, 1 ♀, 2 ♂♂ [AMG]; same data as holotype but date 31.iii.2004 [AMG], 1 ♀ [AMG]; Walvis Bay, 22.ii.1990 (W. J. Pulawski), 6 ♀♀, 2 ♂♂) [CAS]. (All specimens collected by F. W. and S. K. Gess were visiting the pink flowers of *Trianthema hereroensis* Schinz (Aizoaceae: non-Mesembryanthema) or were on the sand immediately next to these plants where resting or mating.)

Geographic distribution.—*Q. femorata* is known only from Namibia, from a single locality on the seaward side of the coastal dunes at the northern extremity of the Southern Namib of Giess (1971).

Floral associations.—*Q. femorata* has consistently been found to be associated solely with *Trianthema hereroensis* Schinz (Aizoaceae: non-Mesembryanthema).

Nesting.—Unknown; probably in the sand beneath the hummock forming *Trianthema* bushes.

Quartinia geigeriae Gess, new species

Diagnosis.—Medium sized to large (3.8–5.0 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Tegula short, laterally rounded, with pos-

terior inner corner a near right angle. Both sexes with angles of propodeum very markedly posteriorly produced, lamellate and subhyaline. Female with head and mesosoma black, tegulae and gaster reddish brown. Male with head, mesosoma and gaster black with yellowish-white markings.

Description.—Female: Black. The following are various shades of reddish brown: labrum; distal two thirds of mandibles; tegula; scutellar lamella; median section of metanotum; in some specimens a narrow streak dorsally on outer aspect of lamellate propodeal angle (rest of lamella subhyaline); terga I–IV or V (narrow posterior bands lighter in colour than rest of terga). Underside of antenna, distal quarter of femur, entire tibia and all tarsomeres of all legs light reddish yellow. Wings hyaline; veins brown.

Length 4.6–5.0 mm (average of 6:4.8 mm); length of fore wing 2.7–3.0 (average of 6:2.9 mm); hamuli 5; length of extended tongue 3.1–3.2 mm.

Head in front view 1.23 × as wide as long, microreticulate but shiny, with separated, moderate sized punctures. POL:OOL = 1:0.85. Clypeus 1.6 × as wide as long (length measured to bottom of emargination; 1.36 × if measured to level of antero-lateral angles), markedly raised anteriorly and laterally, a little flattened medially; anterior margin deeply and evenly emarginate; antero-lateral angles narrowly rounded, lamellate, subhyaline.

Mesosoma microreticulate but shiny; mesonotum and scutellum with punctures slightly larger and sparser than on head; pronotum with punctures similar to those on head; mesopleuron with punctures close together, reticulate-punctate ventrally. Propodeum dorso-laterally markedly raised, dorso-medially depressed to expose metanotum, posteriorly with upper three quarters flat, closely reticulate-punctate and lower quarter unpunctured and shiny, laterally with a smooth, shiny depression and arising from it a very pronounced posteriorly directed lamella; lamella flat, very thin, subhyaline, basally slightly rugose but elsewhere smooth, marginally widely and evenly rounded.

Gaster microreticulate but shiny; punctures finer and shallower than on head and mesosoma, becoming progressively finer posteriorly.

Vestiture generally very short and sparse, longer and more noticeable on labrum, posterior flat surface of propodeum and declivous anterior face of tergum I.

Male: Black. The following are yellowish-white: base of labrum (in some specimens only); clypeal disk and adjoining it a large medial marking on frons together forming an hour-glass-like figure); scape, pedicel and proximal flagellomeres; anterior margin of pronotum (transverse band in some specimens medially interrupted and reduced to two spots); tegula (except for pale testaceous discal spot); in some specimens a narrow streak dorsally on outer aspect of lamellate propodeal angle (rest of lamella subhyaline); narrow posterior bands on terga I–VI (very narrowly anteriorly widened medially on II–VI; immediate vicinity of emargination of tergum VII; distal quarter of femur, entire tibia and all tarsomeres of all legs. Varyingly reddish brown are: mandible distally; concave declivous anterior surface of tergum I. Underside of antennal club light reddish, upper side brown. Wings hyaline; veins brown.

Length 3.8–4.5 mm (average of 6:4.1 mm); length of front wing 2.4–2.8 mm (average of 5:2.6 mm); hamuli 4–5.

Structurally very similar to female but puncturation on gaster noticeably coarser. Tergum VII reticulate punctate, postero-medially with a shallow V-shaped emargination. Parameres postero-laterally smoothly curved to apex; apex not hooked and inner edge of parameres not toothed. Labrum shiny, non-carinate. Antenna with poorly defined, elongate club.

Etymology.—The name *geigeriae*, genitive singular, is formed from the generic name

of the plants, *Geigeria* spp. (Asteraceae), on the capitula of which the wasp was found foraging for nectar or nectar and pollen.

Material examined.—Holotype: ♀, NAMIBIA: Solitaire (23.52S 16.00E), 30.iv.2002 F. W. and S. K. Gess) (visiting yellow flowers of *Geigeria ornativa* O. Hoffm., Asteraceae) [AMG]. Paratypes: NAMIBIA: same data as holotype, 2 ♀♀, 6 ♂♂[AMG]; between Solitaire and Nomtsas (24.15S 16.33E), 1.v.2002 (F. W. and S. K. Gess), 10 ♀♀, 2 ♂♂ (9 ♀♀, 1 ♂ visiting yellow flowers of *Geigeria ornativa*; 1 ♀, 1 ♂ visiting yellow flowers of *Geigeria pectidea* (DC.) Harv.) [AMG]; 1 km N of Mariental (24.37S 17.58E), 2.v.2002 (F. W. and S. K. Gess), 30 ♀♀, 4 ♂♂ (22 ♀♀, 2 ♂♂ visiting yellow flowers of *Geigeria ornativa*; 8 ♀♀, 2 ♂♂ visiting yellow flowers of *Geigeria pectidea*) [AMG]; between Mariental and Keetmanshoop (24.54S 17.55E), 2.v.2002 (F. W. and S. K. Gess), 1 ♂ (visiting yellow flowers of *Geigeria pectidea*) [AMG]; 18 km from Ariamsvlei on road to Aroab [28.00S 19.43E], 14.v.1973 (C. F. Jacot-Guillarmod), 5 ♀♀, 1 ♂ [AMG]; SOUTH AFRICA: NORTHERN CAPE: Langvlei, 103 km WNW of Upington [28.10S 20.16E], 14.v.1973 (C. F. Jacot-Guillarmod), 21 ♀♀, 2 ♂♂ [AMG].

Geographic distribution.—*Q. geigeriae* is known from Namibia, from a limited area in the Semi-desert and Savanna Transition (Escarpment Zone) and the adjoining Dwarf Shrub Savanna of Giess (1971), and from a closely adjoining locality in the Northern Cape.

Floral associations.—Known only in association with two species of *Geigeria*, Asteraceae).

Nesting.—Unknown.

Discussion.—*Q. geigeriae* shares with *Q. artemis* Richards, *Q. breyeri* Richards and the below described *Q. lamellata* the possession of markedly backwardly produced propodeal lamellae. *Q.geigeriae* together with *breyeri* and *lamellata* is readily distinguished from *artemis* in having the posterior inner corner of the tegula rounded or a near right angle, not markedly produced inwards; it is distinguished from both *breyeri* and *lamellata* in having the epicnemium rounded, not defined by a low carina.

Quartinia lamellata Gess, new species

Diagnosis.—Large to very large (5.0–6.2 mm). Fore wing with Cu1a and 2*m-cu* complete and as thick as other veins. Clypeus raised and protruding with, especially in female, marked disto-lateral lobes. Labrum large, very noticeable, in female setose. Epicnemium defined by a low carina. Tegula rounded posteriorly, with posterior inner corner a near right angle. Angles of propodeum markedly backwardly produced, lamellate.

Description.—*Female*: Black. The following are yellowish-white: in some specimens a small spot on disto-lateral lobe of clypeus; transversely oval or bilobed medial marking (in some specimens reduced to two round spots) distally on frons immediately above clypeus; in a single specimen a small round spot in ocular sinus; broad streak behind top of eye; scape (distally), pedicel, intermediate flagellomeres, and underside of antennal club; pair of spots on dorsum of pronotum; large mark on humeral angle (in some specimens remote from spots on dorsum, in others fused with them to form a continuous band); variously developed streak on postero-dorsal angle of pronotum; in some specimens a small spot on mesopleuron; tegula (except for testaceous median area); in some specimens a small streak laterally (flanking tegula) on mesonotum; curved posterior band on disk of scutellum; angles of propodeum; posterior bands, reaching sides and generally slightly expanded medially and laterally, on terga I–V; apical half of tergum VI; postero-lateral corners of sterna II–V and apical half or more of sternum VI; distal half or less of femur, entire tibia and tarsus of all legs. Mandibles, labrum and suffusion on upper surface of antennal club reddish-brown. Wing membrane hyaline; veins brown.

Length 6.0–6.2 mm (average of 3:6.06 mm); length of fore wing 3.9–4.08 mm (average of 3:4.0 mm); hamuli 4.

Head in front view 1.21 × as wide as long. POL:OOL = 1:0.83

Clypeus raised and protruding, medially depressed, distally widely and deeply emarginate and with marked disto-lateral lobes. Labrum large, longer than wide, apically pointed, setose. Clypeus and frons moderately shiny, with close, fairly coarse punctures and finely microsculptured interstices; pronotum, mesoscutum and scutellum with larger, much more sparsely arranged punctures and extremely finely microsculptured interstices; terga uniformly finely punctured. Epicnemium defined by a low carina. Tegula rounded posteriorly. Angles of propodeum markedly backwardly produced, at mid-height forming a rounded projection and below that translucently lamellate.

Male: Black. The following are yellow: clypeus (other than for, in some specimens including holotype, a variously sized median longitudinal marking and in all specimens areas immediately adjacent to antennal sockets); large transverse marking distally on frons immediately above clypeus; broad streak behind top of eye; scape (distally), pedicel, intermediate flagellomeres , and underside of antennal club; most or almost entire dorsal surface of pronotum (except in all specimens small postero-lateral area flanking tegula); spot on mesopleuron; tegula (except for testaceous median area); in all specimens a marking (ranging from a minute spot to a small streak) flanking tegula on mesonotum; curved posterior band on disk of scutellum; scutellar lamella; angles of propodeum; posterior bands (anteriorly ill-defined and grading into reddish-brown), reaching sides on terga I–VI and, to a varying degree, apical half of tergum VII; ill-defined posterior bands on sterna II–VI; most of sternum VII; distal half or less of femur, entire tibia and tarsus of all legs. Mandibles (wholly or in part), labrum and suffusion on upper surface of antennal club, terga and sterna anterior to posterior bands reddish-brown. Wing membrane hyaline; veins brown.

Length 5.0–5.8 (average of 3:5.2 mm; holotype 5.0 mm); length of fore wing 3.0 mm. Head in front view 1.24 × as wide as long

Structurally very similar to female but puncturation on head and mesosoma markedly coarser. Tergum VII with hind margin shallowly emarginate and postero-lateral lobes rounded.

Etymology.—The name *lamellata* is intended to draw attention to the markedly backwardly produced, lamellate angles of the propodeum.

Material examined.—Holotype: ♂, NAMIBIA, Rooibank [23.11S 14.39E], 19.xii.1978 (H. Empey) [AMG]. Paratypes: NAMIBIA: same data as holotype but date 28.xii.1978, 2 ♂♂ [AMG]; Kaokoland [Dist.], Otjinungwa (SE 1712 Ab) [17.17S 12.27E], 19–22.viii.1973 (? collector), 1 ♀ [NNIC]; Kaokoland [Dist.], Khowarib R. (SE 1914 Ac) [locality not pinpointed], 17–19.v.1978 (S. Louw, M.-L. Penrith), 1 ♂ [NNIC]; Namib Naukluft Park, Vogelfederberg (23.03S 15.00E), 21.ii.1988 (G. D. Butler), 1 ♀ [NCP]; same locality, 24.i.1988 (R. Miller and L. Stange), 1 ♀ [FSCA]; Lüderitz [Dist.], Sossusvlei (SE 2415 Cd) [24.43S 15.20E], 12–19.ix.1971 (? collector), 3 ♀♀ [NNIC]; Lüderitz [Dist.], Kanaän 104 (SE 2516 Cc) [25.50S 16.09E], 6–7.x.1972 (? collector), 10 ♀♀ [NNIC];

Geographic distribution.—*Quartinia lamellata* is widespread in the western parts of Namibia, collection localities spanning eight degrees of latitude and falling in the Mopane Savanna, Central Namib and Southern Namib/Semi-desert and Savanna Transition (Escarpment Zone) of Giess (1971).

Floral associations.—Unknown.

Nesting.—Unknown.

Discussion.—See discussion under *geigeriae*. On the basis of the characters there listed, *lamellata* is closest to *breyeri* but may readily be distinguished from that species by its larger size, differently developed clypeus and labrum, differences in puncturation and in colour pattern.

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Torymidae (Hymenoptera: Chalcidoidea) Associated with Bees (Apoidea), with a List of Chalcidoid Bee Parasitoids

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Abstract.—Thirty-one species of Torymidae (Hymenoptera: Chalcidoidea) are associated with bees. In this review each is keyed and discussed, and geographic ranges and hosts are given. Most species are illustrated. Torymids represent about one-fourth of the 135 species of Chalcidoidea associated with bees. Two summary lists are presented for all chalcidoids, including Torymidae, and the 216 bee species with which they are associated. One is arranged as a bee/parasitoid list and the other as a parasitoid/bee list.

Considering that 22,000 species of Chalcidoidea (Noyes 2003) and 16,000–17,000 bee species (Michener 2000) have been described, the number of chalcidoids reported associated with bees is surprisingly small. At most 135 different chalcidoids have been reared from, or associated with, 216 bee species (see Appendix, derived from Noyes 2003). Of these, the families Torymidae and Leucospidae have the highest percentage of the bee parasitoids (each 22–23%), followed closely by Pteromalidae (18%). The other families associated with bees are: Encyrtidae (13%), Eulophidae (13%), Chalcididae (5%), Eurytomidae (5%), Eupelmidae (3%), Mymaridae (0.6%), and Perilampidae (0.6%) (Appendix: based on Noyes 2003).

Although Torymidae and Leucospidae have the highest number of bee parasitoids among Chalcidoidea, this figure is somewhat misleading. Of approximately 1,000 torymid species, only 31 are known (or suspected) to attack bees (Grissell 1995, 2000, 2005; Noyes 2003), so a predilection for bee hosts is not especially pronounced in the family. The host range of this family is extremely broad, but nearly 80% of the known hosts are shared equally between the Hymenoptera and Diptera, most of which are gall-forming cynipids and cecidomyiids (Grissell 1995). Conversely, the entire family Leucospidae, consisting of 135 species, has been presumed to parasitize aculeate Hymenoptera—solitary bees, and less frequently, solitary wasps. In reality, however, hosts are known only for about 30 leucospid species (Bouček 1974, Noyes 2003), so the true relationship of the family to bees is largely unknown. Recently a species of leucospid was reported as an ectoparasitoid of an ichneumonid attacking a cerambycid in limbs of apricot in Iran (Hesami et al. 2005). This finding casts doubt on our concept of host specificity in Leucospidae.

In this paper I present a summary of torymid species reported to attack bees, including a review of published information for each species and a key. I also include a world bee/chalcidoid and chalcidoid/bee list for all Chalcidoidea reportedly associated with bees (Appendix).

As with many chalcidoid records, the true host is not always indicated by the host record given (Noyes 1994). Many bee host records are simply nest rearings and may have been contaminated by other true parasitoids, cleptoparasitoids, inquilines, and simple space usurpers of all sorts, many not even hymenopteran. Similarly, a mud wasp's nest may be usurped by a nesting bee, thus causing confusion as to the true host (Rust 1974). Bee nests, as well as almost any other ecological niche, offer complex arrays of hosts, many of which are not even suspected at the time of rearing. For example, *Glyphomerus stigma* (Fabricius) was reported from *Melitoma taurea* (Say) (Apidae), but this is likely to be an error because all other records for species of *Glyphomerus* are gall-forming cynipids or rarely eurytomids (Grissell 1995). With respect to bee parasitoids, therefore, all records should be considered tentative until established by dissection and observation. Within the Torymidae listed in this paper, I point out that several are likely not to be true bee parasitoids. In those few cases where the biologies of torymids are known they are generally solitary, idiobiotic larval ectoparasitoids, but in several genera (e.g., *Monodontomerus*, *Microdontomerus*) larvae are known to be gregarious (Grissell 2000, 2005).

In examining host records presented in the Appendix several reviewers suggested that it might be informative to summarize parasitoid data with respect to bee biology as there appeared to be a bias towards twig and cavity nesting bees, with ground-nesters being under-represented. I solicited the input of two recognized bee authorities: Frank Parker, who specializes in twig-nesters, and Jerry Rozen, who specializes in ground-nesters, and both agreed that the data suggested cavity nesters were the predominant host representatives. These are primarily twig nesters, bees that nest in pre-existing crevices or cavities, and bees that re-use old bee nests. Some of these nests may be external, for example resin nests attached to objects such as twigs and rocks. According to Rozen most of the records are indicative of shallow nesting bees, and he suggested that ground nesting bees in general would be less likely to harbour parasitoids because they might have a more difficult time entering nests and crawling down the "... long, main tunnels" to find their host. He also pointed out that old bee nests and shallow cavities are frequently re-used several times, thus encouraging the build-up of large parasitoid populations. Parker suggested that twig-nesting bees are more likely to be sampled because they readily come to artificial traps set out by the collector. They are also easier to extricate and study in these nests. Conversely, ground nesting bees must be actively hunted by the collector, are less easily found, and require painstaking excavation to reveal nest details.

In general, then, records summarized in the Appendix indicate that host data are biased towards parasitoids attacking cavity nesting bees and that multiple causes contribute to this bias. Whatever cursory glimpses the bee/parasitoid host list may reveal, and considering the numerical size of the chalcidoid and apoid groups, it appears that much remains to be discovered. Within existing literature, relatively little is devoted to parasitization and then primarily only to a few solitary bee species (e.g., the alfalfa leafcutting bee, Stolbov et al. 1986), whereas with few exceptions (e.g., Zerova and Romasenko 1986) there is scarcely any comprehensive literature pertaining to solitary bee parasitoids.

METHODS

In the following discussions host names are given without authors. Complete authors' names may be found in the Appendix. Within discussions, hosts are listed alphabetically by family, but in the host listing all hosts are alphabetic regardless of family.

KEY TO TORYMIDAE ASSOCIATED WITH SOLITARY BEES

1 Anterior edge of metapleuron straight, not projecting forward as lobe into mesepimeron (Fig. 2) 4

— Anterior edge of metapleuron (usually its upper half) projecting forward as lobe into mesepimeron (Fig. 1), which is subdivided into upper and lower sections, lower section delimited by anterior groove ..... *Torymus* Dalman 2

2 Hind coxa dorsally covered with short setae (Fig. 3), coarsely reticulate; propodeum areolate-rugose, heavily carinate (Fig. 5); frenal area less than 1/5 length of scutellum (Fig. 7) 3

— Hind coxa dorsally bare (a few long setae may be present; Fig. 4), smooth and polished; propodeum essentially smooth (Fig. 6); frenal area 1/3 to almost 1/2 length of scutellum (Fig. 8) (Palearctic, Australasian [?introduced]) ..... *Torymus armatus* Boheman

3(2) Head dorsum, mesosoma, and hind coxa coppery with greenish tints; at least part of hind femur orange, concolorus with tibia (Palearctic) ... *Torymus cupreus* (Spinola)

— Head dorsum, mesosoma, and hind coxa metallic green or blue; entire hind femur metallic green or blue, contrasting with orange tibia (Nearctic) ..... *Torymus zabriskii* (Cresson)

4(1) Fore wing with marginal and stigmal veins conspicuously thickened relative to submarginal vein, postmarginal vein not projecting beyond tip of stigmal vein (Figs 9, 12, 13), and with marginal vein slightly removed from margin of wing (Fig. 13; may be somewhat difficult to see); malar distance longer than intermalar distance (Figs 14, 15); mandibles reduced, scarcely visible, tips not meeting medially when closed, apically without teeth ..... *Echthrodape* Burks 5

— Fore wing with marginal and stigmal veins not conspicuously thickened relative to submarginal vein, with postmarginal vein longer than stigmal vein (Fig. 10), and with marginal vein at edge of wing margin; malar distance subequal to or shorter than intermalar distance (Fig. 11); mandibles visible, tips meeting medially when closed, apically with teeth 6

5(4) Postmarginal vein developed, longer than stigmal vein, which is slender and petiolate (Fig. 12); genae straight, not concave (Fig. 14) [Papua New Guinea, Australia] ..... *Echthrodape papuana* Bouček

— Postmarginal vein reduced, subequal to stigmal vein, which is thick and sessile (Fig. 13); genae concave (Fig. 15) [Kenya] ..... *Echthrodape africana* Burks

6(4) Occipital carina absent (Fig. 16), weakly or questionably developed, or if apparent, then medially arched and midway between hind ocelli and occipital foramen and not reaching hypostomal carina (Fig. 17) (head usually vertical with dorsoposterior aspect slightly concave and the carina, if present, easily seen); hind femur slender, apicoventrally either without tooth (Fig. 34), angulate, or vaguely serrate; metasomal terga with or without apicomedian emarginations, often weakly sclerotized 26

— Occipital carina well developed, dorsal margin not greatly arched but nearly horizontal (Fig. 18), closer to occipital foramen than to hind ocelli and reaching hypostomal carina (head usually tilted forward with dorsoposterior aspect conspicuously concave and occipital carina easily seen, but head must be removed to see hypostomal carina); hind femur apicoventrally with abrupt tooth (Figs 35, 37, 38), or greatly swollen and angulate (Fig. 36); metasomal terga heavily sclerotized, without apicomedian emarginations [Holarctic, Neotropical, Oriental] ..... *Monodontomerus* Westwood 7

7(6) First 2 flagellar segments reduced in length, ring-like (Fig. 19); hind femur swollen with distal subapical angle but without distinct tooth (Fig. 36) [Nearctic] ..... *Monodontomerus thorpi* Grissell

— At most, first flagellar segment reduced in length (Fig. 20); hind femur relatively narrow with distinct subapical tooth (Figs 37, 38) 8

8(7) Female, face transverse, intermalar distance 3.5 to 5× length of malar distance; male, face grotesquely modified, entirely sunken medially (as if entirely consisting of scrobal basin) (Fig. 22), with sharp edge mesad of eye (Fig. 21) [Palearctic, Nearctic (introduced)] ..... *Monodontomerus osmiae* Kamijo

— Both sexes, face at most slightly transverse, intermalar distance from 1 to 3× length of malar distance; male with face not medially sunken, scrobal basin normal, though areas on either side of scrobe may be slightly depressed 9

9(8) Clypeus greatly elongate (Figs 23, 24) [Palearctic] .. *Monodontomerus anthidiorum* Lucas

— Clypeus either barely reaching to or beyond line drawn across lateral corners of oral fossa (Figs 25–28) 10

10(9) Upper mesepimeral area with anterior half reticulately sculptured and anterodorsal corner diagonally striate extending nearly to transepimeral sulcus (Fig. 53) 11

— Upper mesepimeral area nearly entirely polished with striae scarcely extending half way to transepimeral sulcus (Figs 54, 55) 12

11(10) Discal setae of fore wing not extending into basal area (as in Fig. 31); female with ovipositor sheaths shorter than metasoma; male with clypeus recessed (not extending beyond line drawn across lateral corners of oral fossa), malar sulcus absent or obscure, malar distance subequal to intermalar distance; scape with ventral surface slightly keeled vertically (i.e., not flat), no pores visible [Palearctic] ..... *Monodontomerus laticornis* Grissell and Zerova

— Discal setae of fore wing extending into basal area (as in Fig. 29); female with ovipositor sheaths as long as or longer than entire body; male with clypeus extending beyond line drawn across lateral corners of oral fossa, malar sulcus present; malar distance about 1.5× intermalar distance; scape with ventral surface flat, covered with pores visible at 100× [Nearctic] ..... *Monodontomerus clementi* Grissell

12(10) Metasomal tergum 2 dorsally with reticulate to strigate sculpture in distal half ... 13

— Metasomal tergum 2 dorsally smooth, polished in distal half 14

13(12) Distal portion of postmarginal vein equal in length to proximal portion (as in Fig. 30); rim of scutellum apically widened, somewhat projecting; females, metasomal tergum 6 acute in profile (as in Fig. 32); male, fore leg unmodified (i.e., normal) (as in Fig. 39), tibia equal in length to femur and not ventrobasally concave, tarsomeres elongate (claw length equal to or shorter than tarsomere 4) [Nearctic] ..... *Monodontomerus dianthidii* Gahan

— Distal portion of postmarginal vein 0.33× length of proximal portion (as in Fig. 31); rim of scutellum apically even in width, not projecting; female, metasomal tergum 6obtuse in profile (as in Fig. 33); male, fore leg modified (Fig. 40), tibia shorter in length than femur and ventrobasally concave, tarsomeres shortened (claw length equal to tarsomeres 3 and 4) [Nearctic] ..... *Monodontomerus brevicrus* Grissell

14(12) Malar sulcus absent (Fig. 28), or if weakly apparent, greatly curved backward from lower margin of eye then curving downward to join edge of malar opening (Fig. 27); lower face protuberant in profile (Fig. 28) [Nearctic] ..... *Monodontomerus bakeri* Gahan

— Malar sulcus well developed, straight (Figs 25–26), or slightly curved from lower margin of eye to lateral edge of malar opening; lower face flat (not bulging) in profile (Fig. 26) 15

15(14) Frenal area medially highly polished, appearing glabrous, faint coriaceous sculpture may be seen with difficulty at some angles of view (questionable species will run through either couplet of key) 16

— Frenal area medially sculptured, may be uniformly similar overall or relatively less prominent than laterally, never glabrous, sculpture easily visible at any angle of view (questionable species will run through either couplet) 19

16(15) Costal cell above with apical setal row incomplete, confined to distal 1/2 or less of cell (as in Fig. 31); female, metasomal tergum 6 strongly concave in profile (as in Fig. 32) [Nearctic] ..... *Monodontomerus torchioi* Grissell (most specimens)

— Costal cell above with apical setal row complete (as in Fig. 29); female, metasomal tergum 6 weakly concave in profile (as in Fig. 33) 17

17(16) Frenal area apicomedially intruding into rim, punctures of rim reduced in size at point of intrusion (Fig. 42); stigma and uncus relatively short, postmarginal vein with proximal and distal section subequal in length (Fig. 30) [Holarctic] ..... *Monodontomerus aeneus* (Fonscolombe)

— Frenal area with apical rim not interrupted posteriorly at median margin, punctures of rim as large or larger at apex as on sides (as in Fig. 41); stigma and uncus elongated, postmarginal vein with proximal section longer than distal (as in Fig. 31) 18

18(17) Female ovipositor sheaths swelling distally (i.e., not parallel-sided); male hind femur broad, widening apically, about 2.5× as long as wide (Fig. 38) [Palearctic] ..... *Monodontomerus rugulosus* Thomson

— Female ovipositor sheaths same width throughout (i.e., parallel-sided); male hind femur narrow, dorsal and ventral margins essentially parallel (Fig. 37), about 3.5× as long as wide [Neotropical] ..... *Monodontomerus argentinus* Brèthes

19(15) Costal cell above with apical setal row complete (Fig. 29) 20

— Costal cell above with apical setal row incomplete, confined to distal 1/3 to 1/2 of cell (Fig. 31) or appearing absent (2 or 3 setae may be present at apex as in Figs 43, 44) ... 22

20(19) Scape about 4× longer than wide, greater in length (about 1.3×) than distance from venter of torulus to apical margin of clypeus [Nearctic, Neotropical] ..... *Monodontomerus mexicanus* Gahan

— Scape about 3× longer than wide, subequal in length to distance from venter of torulus to apical margin of clypeus 21

21(19) Stigma rectangular, proximally elongated towards base of wing (Figs 51, 52); postmarginal vein with distal length less than proximal length (Figs 51, 52); male face with depression laterad of scrobal basin [Nearctic] ..... *Monodontomerus acrostigmus* Grissell

— Stigma squarish, neither stigma nor proximal angle elongated (as in Figs 10, 44); postmarginal vein with distal length subequal to basal length (as in Fig. 44); male face convex laterad of scrobal basin [Holarctic] ..... *Monodontomerus obscurus* Westwood

22(19) Admarginal setae reaching bases of marginal vein and parastigma (Fig. 43); intermalar distance subequal to 3× malar distance (Fig. 48); both mandibles with single apical tooth and small secondary tooth on dorsal margin (Fig. 48) [Nearctic] ..... *Monodontomerus mandibularis* Gahan

— Admarginal setae either not reaching base of marginal vein or apex of parastigma (Fig. 44); intermalar distance less than 2.5× malar distance (Fig. 47); both mandibles with 2 apical teeth, and small third tooth on dorsal margin (Figs 47) 23

23(22) Transepimeral sulcus incomplete (Figs 53, 55); upper anterior margin of costal cell with setal row in apical 1/4 to 1/3 (as in Fig. 31); male, scape in side view slightly curved in profile (Fig. 56), area beneath torulus flat, sculptured, and setose 24

— Transepimeral sulcus complete (Fig. 54), appearing as a sculptured groove; upper anterior margin of costal cell with 1 to 3 setae at apex (Figs 43, 44); male, scape in lateral view strongly C-shaped (Figs 57, 58), area beneath torulus slightly swollen, polished, and asetose 25

24(23) Frenal area medially with reticulate sculpture readily apparent, area may be shiny, but sculpture visible at any angle of view; male, ventral surface of scape without pores visible at 100× [Nearctic] ..... *Monodontomerus montivagus* Ashmead

— Frenal area medially with reticulate sculpture visible only at some angles of view and seen only with difficulty, area shiny and appearing polished; male, ventral surface of scape evenly covered with pores easily visible at 100× [a few atypical specimens run here, but most to couplet 16 based on the polished frenal area] [Nearctic] ..... *Monodontomerus torchioi* Grissell

25(23) Females, ovipositor subequal to metasoma (ca. 1–1.2×); scape orange to yellow without metallic infusion especially ventrally; male, scape greatly laterally compressed (ventral and dorsal surfaces essentially absent), outer surface flat, polished, asetose, and curving smoothly to inner surface without interruption (Fig. 57), no pores visible at 100× [Nearctic] ..... *Monodontomerus parkeri* Grissell

— Females, ovipositor obviously longer than metasoma (ca. 1.5–1.8×); scape with metallic green infusion at least ventrally (may be complete or confined to area just beneath pedicel); male, scape dorsoventrally compressed, curved, with dorsal and ventral surfaces parallel and delimited by right-angled edge (Fig. 58), ventral surface polished and covered with pores visible at 100× though difficult to see [Nearctic] ..... *Monodontomerus tepedinoi* Grissell

26(6) Marginal vein long, 3–7× length of postmarginal vein and at least 6× length of stigmal vein; occipital carina present, its lateral edges extending at least in line with *dorsum* of hypostomal foramen [Oriental] ..... *Pseudotorymus indicus* (Mani)

— Marginal vein short, 1–2.5× length of postmarginal vein and 2–5× length of stigmal vein (Figs 45, 46); occipital carina absent (Fig. 16) or, if present, its lateral edges not (or scarcely) extending in line with *venter* of occipital foramen (Fig. 17) 27

27(26) Occipital carina absent (Fig. 16) ..... *Microdontomerus* Crawford 28

— Occipital carina visible in dorsal view as finely polished line raised distinctly above surface sculpture (as in Fig. 17) [Palearctic] .... *Adontomerus* Nikol'skaya (*A. gregalis* (Steffan) and *A. nesterovi* Zerova)

28(27) Fore wing setation (Figs 45, 46) reduced; basal cell open behind, i.e., cubital vein basally at most with few isolated setae; basal vein at most with isolated setae; basal cell without distinct setal row paralleling submarginal vein 29

— Fore wing setation (as in Figs 29, 31) not reduced (except in admarginal area of some species): basal cell closed behind, i.e., cubital vein essentially completely setose to base of wing; basal vein with distinct setal row and basal cell with setal row paralleling nearly entire submarginal vein 30

29(28) Postmarginal vein (Fig. 46) about 0.75× as long as marginal vein; fore wing with admarginal area (Fig. 46) not well defined posteriorly by setal line, with admarginal setae nearly as uniform as central area of wing [Nearctic] .... *Microdontomerus enigma* Grissell

— Postmarginal vein (Fig. 45) about 0.5× as long as marginal vein; fore wing with admarginal area (Fig. 45) well-defined posteriorly by setal line, with few sparse setae not as uniform as central area of wing [Nearctic] .... *Microdontomerus parkeri* Grissell

30(28) Eye height nearly 3× malar distance (Fig. 49); distance between eyes less than eye height (Fig. 49) [Nearctic] ..... *Microdontomerus anthidii* (Ashmead)

— Eye height 2.5× or less than malar distance (Fig. 50); distance between eyes equal to eye height (Fig. 50) [Nearctic] ..... *Microdontomerus apianus* Grissell

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Adontomerus Nikol'skaya

Recognition.—*Adontomerus* is recognized by the straight anterior edge of the metapleuron (Fig. 2); the fore wing with marginal vein 1 to 2.5× the length of the postmarginal vein, 2 to 5× the length of the stigmal vein, and marginal + postmarginal veins equal to 0.2× the length of the wing; the occipital carina visible in dorsal view as a finely polished line raised distinctly above surface sculpture, medially arched

and midway between hind ocelli and occipital foramen (Fig. 17); and the hind femur ventrally without a tooth (as in Fig. 34).

Number of Species.—8.

Number Associated with Bees.—2.

Distribution.—Species of this genus are reported in the Palearctic Region including the former Soviet Union, Bulgaria, former Yugoslavia, Hungary, Italy, Sardinia, Spain, Jordan, and Algeria.

Hosts of Genus.—Species of *Adontomerus* have been reared from cocoons of Lasiocampidae (Lepidoptera), galls of Cynipidae (Hymenoptera), and cocoons of Megachilidae (Hymenoptera). In the National Museum of Natural History, Washington, DC, there are specimens reared from weevils in seed heads of Asteraceae.

Discussion.—Records for the species listed below have been cited in the literature under the genus *Mellitotorymus*, which was synonymized with *Adontomerus* by Grissell (1995).

Adontomerus gregalis (Steffan)

Distribution.—PALEARCTIC: Reported only from Sardinia (Steffan 1964).

Host.—Reared from *Pseudoanthidium* (reported as *Anthidium*) *lituratum* (Megachilidae).

Discussion.—I believe that this species and *Adontomerus nesterovi* are synonyms, but I have not seen material of the latter to confirm this. Both share essentially similar descriptions as well as the same host. I treat them separately here to retain the known data, but there is no way to distinguish the species as far as I can tell.

Adontomerus nesterovi Zerova

Distribution.—PALEARCTIC: Reported from Turkmenistan (Zerova and Romasenko 1986).

Host.—Reared from cocoons of *Pseudoanthidium* (as *Paraanthidiellum*) *lituratum* (Megachilidae).

Discussion.—Zerova and Romasenko (1986) keyed and figured this species in a paper on the parasitoids of megachilid bees in the former Soviet Union.

Echthrodape Burks

Recognition.—*Echthrodape* is recognized by the straight anterior edge of the metapleuron (as in Fig. 2) and by the relatively short wing venation and the thickened marginal vein (Figs 9, 12, 13), with the postmarginal vein some distance from the distal edge of the wing (Fig. 9). Additional characters that help in recognition are the toothed hind femur (as in Fig. 38), the developed occipital carina that lies midway between the hind ocelli and occipital foramen, and the reduced mouth opening (Figs 14, 15, indicated, in part, by the long malar distance) with reduced mandibles (scarcely visible and obscured by other mouth parts).

Number of Species.—2.

Number Associated with Bees.—2.

Distribution.—The genus is found in the Afrotropical Region in Kenya, and in the Australasian Region from Papua New Guinea.

Host.—Hosts for both species belong to the genus *Braunsapis* (Apidae).

Discussion.—The species of this genus are uncommonly encountered and are presently the only indigenous torymid bee parasitoids known from sub-saharan Africa and Australasia. The lack of records for these areas is probably the result of a paucity of collecting and rearing both bees and parasitoids.

Echthrodape africana Burks

Distribution.—AFROTROPICAL: Reported from Kenya (Burks 1969).

Host.—Reared from nests of *Braunsapis* (as *Allodapula*) (Apidae) as reported by Burks (1969) and expounded upon by Michener (1969) who reported the following host records: *Braunsapis simplicipes*, *B. rolini*, and *B. rufipes*.

Biology.—Larvae of *E. africana* are external feeders on pupae of *Braunsapis* (Michener 1969). One parasitoid was seen per host. The bee is a progressive feeder which uses burrows in the pith of dead *Lantana* stems. It moves its larvae and pupae about and does not distinguish between its own progeny and those of *E. africana*.

Morphology.—Michener (1969) illustrated and described the peculiar larva of this species as well as the pupa.

Discussion.—The two known species are relatively easily identified based on the distinctive heads (Figs 14, 15) and wing veins (Figs 12, 13) as well as their disjunct distributions.

Echthrodape papuana Bouček

Distribution.—AUSTRALASIAN: Known from Papua New Guinea (Bouček 1988) and Australia (R. Matthews, per. comm.).

Host.—Reared from cells of *Braunsapis unicolor* (Apidae) nesting in bamboo internodes (R. Matthews, per. comm.).

Discussion.—A voucher specimen for the Australian record was kindly placed in the U. S. National Museum collection by Robert Matthews.

Microdontomerus Crawford

Recognition.—Microdontomerus is recognized by the straight anterior edge of the metapleuron (as in Fig. 2), the simple hind femur (as in Fig. 34), the absence of an occipital carina (Fig. 16), and the marginal vein short, 1 to 2.5× the length of the postmarginal vein and 2 to 5× the length of the stigmal vein (Figs 45, 46).

Number of Species.—22.

Number Associated with Bees.—4.

Distribution.—This genus is transcontinental in the Nearctic, but limited in other regions of the world. In the Palearctic it is found in Spain, Italy, Algeria, and Libya, and in the Afrotropical Region it is found in Senegal. [The genus was reported in India (see Farooqi 1986, David et al. 1990), but this is probably a misidentification resulting from the confusion in names that existed at the time.]

Hosts.—Species are reported from megachilid bees and cynipid gall-formers (Hymenoptera), tephritids (Diptera), buprestid eggs and curculionids (Coleoptera), mantid eggs (Mantodea), and coleophorids, gelichiids, lasiocampids, and tortricids (Lepidoptera). At least one Nearctic species attacks saturniid eggs (Lepidoptera). Species have also been documented as facultative hyperparasitoids of braconids (Hymenoptera) (Grissell 2005).

Microdontomerus anthidii (Ashmead)

Distribution.—NEARCTIC: This species has been collected in southern California, USA.

Host.—Reared from *Dianthidium pudicum consimile* (as *Anthidium consimile*) (Megachilidae).

Discussion.—Microdontomerus anthidii, *M. enigma*, and *M. parkeri* are difficult to distinguish. Generally *M. anthidii* is smaller (2.3 mm or less) with a shorter ovipositor (less than 1.2× hind tibia), whereas *M. parkeri* is larger (up to 3.0 mm) with a longer ovipositor (more than 2× hind tibia). *Microdontomerus enigma* is about the size of *M. anthidii*, but with the longer ovipositor of *M. parkeri*. *Microdontomerus anthidii* is fairly easily separated from the other two, however, based on discrete morphological differences in the fore wing: *M. anthidii* has a complete setal row along the upper anterior margin of the costal cell (absent in the other two species) and the basal cell is closed (open in the other two species). It appears that while all three species attack megachilid bees, *M. anthidii* is usually associated with species of the tribe Anthidiini that create nests of resin and sand grains, whereas *M. parkeri* and *M. enigma* are associated with Osminiini and Megachilini that make stem nests.

Microdontomerus apianus Grissell

Distribution.—NEARCTIC: Known from California, USA.

Host.—Reared from *Megachile montivaga* (Megachilidae).

Discussion.—In addition to characters given in the key, this species differs from *M. anthidii* in having the intermalar distance about 1.7× the malar distance (about 2.5× in *M. anthidii*), and in having the ovipositor sheaths subequal to the body length and 2.0–3.0× as long as the hind tibia (in *M. anthidii* ovipositor sheaths subequal to metasoma and usually less than 1.5× as long as hind tibia).

Microdontomerus enigma Grissell

Distribution.—NEARCTIC: Known only from one locality in Nevada, USA.

Hosts.—Reared from *Hoplitis bullifacies* (Megachilidae).

Discussion.—This species is phenotypically nearly identical to *M. parkeri*. Characters to separate the two are given in the key. Somewhat more difficult to assess is that in *M. enigma* the longest diameter of the lateral ocellus is less than the ocellocular distance, whereas it is subequal to or greater than the distance in *M. parkeri*.

Microdontomerus parkeri Grissell

Distribution.—NEARCTIC: Widespread in the western and southwestern United States.

Hosts.—Reared from Megachilidae: *Ashmeadiella bigeloviae*, *Ashmeadiella cubiceps*, *Ashmeadiella gillettei*, *Ashmeadiella rufipes*, *Hoplitis bullifacies*, *Hoplitis palmarum*, *Megachile brevis*, and *Osmia marginata*.

Biology.—*Microdontomerus parkeri* is a gregarious parasitoid within individual bee cells. The number of individuals ranged from 2 to 33 per cell, with an average of about 8–9. For these rearings the total number of *M. parkeri* specimens was 229 females and 125 males for a sex ratio of 1.8 to 1. Ten of these rearings contained no males (Grissell 2005).

Discussion.—This species has also been reared from *Ancistrocerus* sp. and *Leptochilus* sp. (Vespidae: Eumeninae). It is the most common and widespread species of *Microdontomerus* attacking bees.

Monodontomerus Westwood

Recognition.—*Monodontomerus* is recognized by the straight anterior edge of the metapleuron (as in Fig. 2), the presence of a frenal line on the scutellum (as in Fig. 8), the hind femur with a single, apicoventral tooth (Figs 35, 37; though in one species this tooth is poorly defined, Fig. 36), and by the well developed occipital carina which is nearly horizontal on its dorsal margin and closer to the occipital foramen than to the hind ocelli (Fig. 18).

Number of Species.—32.

Number Associated with Bees.—19.

Distribution.—The species of this genus are widespread throughout the Holarctic, and somewhat less common in the Neotropical (Cuba, Mexico, Colombia, Argentina) and Oriental (Sri Lanka, India, Pakistan) regions.

Hosts.—Numerous hosts are known for this genus including families in Diptera, Hymenoptera, and Lepidoptera. The primary hosts are solitary aculeate bees and wasps, sawflies, and moths (including their tachinid and ichneumonid parasitoids). An authentic record of *Monodontomerus* (undetermined species) attacking social vespids (*Mischocyttarus*; Litte 1979) in Arizona occurs in the literature, but voucher specimens are now lost (Litte, *in litt.*). Unfortunately, some species of *Monodontomerus* are extremely difficult to tell apart and as a consequence there have been many misidentifications resulting in incorrect host records for some species. For example, *Monodontomerus aereus* Walker has been reported from *Megachile muraria* (now = *M. parietina*)(Constantineanu et al. 1956), but this would not be considered a host based on the majority of records, which are from Lepidoptera (Grissell 2000, Noyes 2003). *Monodontomerus vicicellae* (Walker), a common parasitoid of larval

Lepidoptera and sawflies, was reported to be reared from an ichneumonid parasitoid in the nest of *Megachile "ramulorum* Rond." (Rondani 1877), which is a *nomem nudum*. There are no other records from bees for this species and the host record is considered to be incorrect. Similarly, *Monodontomerus minor* (Ratzeberg), also a parasitoid of Lepidoptera and sawflies, has been reported from several bees, but while these records appear in lists (e.g., Herting 1977) they apparently have no basis in the primary literature.

Discussion.—In the following section, summary data are documented in Grissell (2000) unless otherwise specified. Identification is often more easily based on male characters. Although females predominate in reared series, species have gregarious larvae and some males are almost always present.

Monodontomerus acrostigmus Grissell

Distribution.—NEARCTIC: Eastern Texas, USA.

Hosts.—Reared from pupa of *Megachile* sp. (Megachilidae) in a "mud-dauber nest".

Discussion.—*Monodontomerus acrostigmus* is similar in appearance to *M. obscurus*, but differs from it (and all other known species) by having the stigma posteriorly appendiculate (Figs 51, 52). In addition, it differs from *M. obscurus* by having the distal portion of the postmarginal vein one half or less than the proximal portion (subequal in *M. obscurus*) and in males, which have the face lateral to the scrobal basin distinctly depressed (not depressed in *M. obscurus*).

Monodontomerus aeneus (Fabricius)

Distribution.—NEARCTIC: Widespread throughout the northern United States and southern Canada. PALEARCTIC: Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and often confused with *M. obscurus*, which has the same distribution and general host range.

Hosts.—There are a great number of hosts listed for this species (as *obsoletus*) in the Old World (see Grissell 1995). Only bee hosts are listed here because these are certainly correct whereas all other hosts are suspect. Old World: *Anthophora retusa*, *Ceratina callosa* (Apidae); *Anthidium florentinum*, *Hoplitis* (as *Osmia*) *adunca*, *Megachile parietina* (as *Chalicodoma muraria*) (and *Stelis nasuta*, a cleptoparasite of this host), *Megachile apicalis*, *Megachile centuncularis*, *Megachile* (as *Chalicodoma*) *sicula*, *Osmia* (as *Metallinella*) *brevicornis*, *Osmia coerulescens*, *Osmia rufa cornigera*, *Osmia cornuta*, *Osmia emarginata*, *Osmia fulviventris*, *Osmia latreillei*, *Osmia rufa*, *Osmia submicans*, *Osmia tricornis* (all Megachilidae). New World: Verifiable records for this species include *Megachile concinna*, *Megachile rotundata*, and *Osmia nigrifrons* (Megachilidae).

Biology.—Newport (1849, 1852, 1853) provided information and illustrations of the larvae, their digestive tract, and feeding habits. Johansen and Eves (1966) and Eves (1970) (and possibly Hobbs and Krunic 1971) published biological information on this species (as *obscurus*, reidentified by me, based upon Eves' specimens) as a parasitoid of *Megachile rotundata*. Females oviposited through the leaf-lined cell and/or cocoon of the host. Between 3 and 51 eggs were laid externally on the host. An average of 10 survived in one study (Johansen and Eves 1966), but Bonelli and Campadelli (1990) gave an average of 24 (range = 10 to 51 adults for 15 bee cells). All immature stages of the host are vulnerable to attack but parasitization of early instars is rarely successful. Larvae are non-cannibalistic. The life cycle can be completed in about 20 days. Goodpasture (1975) detailed the mating behavior of *M. aeneus* (reported as *M. obscurus*, but subsequently confirmed as *M. aeneus* in Grissell 2000). Tepedino (1988a) demonstrated that 7–12% of females mated before emergence from the host cocoon. He also

showed (Tepedino 1988b) that females had an initial obligatory requirement for host cocoon and prepupal authenticity, but after 24 hours this would break down and females would oviposit into gelatin capsules holding bee prepupae or even agar replicates of bees. Females oviposited onto fresh host prepupae or prepupae that were up to 16 days old. Tepedino (1988c) showed that superparasitism occurs but that rates go down as resident parasitoids become older. In Spain, rates of parasitism for *M. aeneus* (reported as *M. obsoletus*) on *Osmia cornuta* (Megachilidae) varied from 0.5% (Bosch 1994b) to 73% (Bosch 1994a). According to Bosch (1993) 53–76% of managed bee cocoons were parasitized when paper straws containing bee cells were extracted from their nesting blocks, but cells left in grooved boards were left untouched. In the Nearctic this parasitoid (as *M. obscurus*) reportedly replaced the native species *M. montivagus* in the mid-1960's as the most important parasitoid of the alfalfa leafcutting bee in North America, but then was itself replaced by a pteromalid in the mid 1970's (Eves 1982). A paper on control of an unknown species of *Monodontomerus* in Utah by Brindley (1976) undoubtedly refers to this species.

Morphology.—Goodpasture illustrated the karyotype of *M. obsoletus* (1975, reported as *M. obscurus* but confirmed as *M. aeneus* by Grissell 2000). The chromosomes number 4 in males, 8 in females. Goodpasture (1975) illustrated male scapes, and Walther (1983) illustrated antennal sensillae of this species.

Discussion.—This species was introduced into the Nearctic in the 1930's (Johansen and Eves 1966), but it was misidentified as *M. obscurus.* Its correct identity as *M. obsoletus* was reported by Tepedino (1989) based upon my identification. The name has since been changed to *M. aeneus* by Graham (1992) who studied the type material of the species involved. Almost all previously published host records (e.g., Peck 1969) for *M. obscurus* are wrong and most should now refer to *M. aeneus*. Both *M. aeneus* and *M. obscurus* are common and widespread and are among the two most difficult species of the genus to distinguish from each other. This is disconcerting because they are economically important, have both been introduced into the New World along with the alfalfa leafcutter bee, and have been confused with each other since their introductions. Only the apparent absence of sculpture (though faint coriaceous sculpture may be apparent at some angles of view) on the median frenal area and the construction of the frenal apex offer reliable diagnostic information to separate these two species, but even this can be difficult to interpret on occasion. An additional character that may sometimes help to define these two taxa is found in the mesepimeron. In *M. aeneus* the entire mesepimeron is essentially smooth (polished) except for some slight reticulation (or carinae) above the ventral margin. In *M. obscurus* the ventral 1/5 of the mesepimeron below the transepimeral sulcus is reticulate and the anterior 1/3 is alutaceous to lightly reticulate.

Monodontomerus anthidiorum (Lucas)

Distribution.—PALEARCTIC: Found only in Algeria.

Host.—Reared from *Rhodanthidium sticticum* (Megachilidae).

Biology.—This species was reared from the larva of its host. According to Lucas (1849) the bee nested in empty snail shells (*Helix* spp). The larvae were gregarious with 40–50 specimens of *M. anthidiorum* found in each shell.

Discussion.—This species apparently has not been collected since its original description. In both sexes this is one of the most distinct species of the genus based on the elongated clypeus (Figs 23, 24).

Monodontomerus argentinus Brèthes.

Distribution.—NEOTROPICAL: Costa Rica, Panama, Colombia, and Argentina.

Hosts.—Reared from cells of *Eufriesea nigrescens* (as *Euplusia longipennis*) (Apidae) in Colombia. A species of *Megachile* (Megachilidae) also serves as host.

Biology.—Sakagami and Sturm (1965) reported that this species developed on the pupal stage.

Discussion.—*Monodontomerus argentinus* is similar to *M. mexicanus* especially in proportions of the head and antenna and in details of the wing. In both sexes of *M. argentinus* the median area of the frenum is highly polished, whereas in *M. mexicanus* the median frenal area is longitudinally sculptured similar to the lateral areas.

Monodontomerus bakeri Gahan

Distribution.—NEARCTIC: Colorado, Utah, Idaho, USA, and Alberta, Canada.

Hosts.—*Megachile pugnata*, *Megachile relativa*, *Megachile rotundata*, *Osmia coloradensis*, and *Osmia texana* (Megachilidae).

Discussion.—This species is relatively uncommon, but large numbers were trapped from *Megachile rotundata* blocks as a nuisance species at the USDA Bee Biology and Systematics Laboratory in Logan, Utah (pers. obs.). *Monodontomerus bakeri* is unique among species of the genus in two ways. The absence of a malar sulcus (Fig. 28), or its expression as a greatly curving, indefinite line (Fig. 27), is atypical compared to the straight, well-defined sulcus found in most other species (e.g., Fig. 26). Also, the bulging lower face (Fig. 27) is not found in any other species, all of which have the area essentially flat (as in Fig. 26).

Monodontomerus brevicrus Grissell

Distribution.—NEARCTIC: California, USA.

Hosts.—Reared from nests of *Osmia ribifloris* (Megachilidae).

Discussion.—*Monodontomerus brevicrus* resembles *M. dianthidii* in having metasomal tergum 2 dorsally sculptured, but it is separated as follows: Both sexes of *M. brevicrus* have the distal portion of the postmarginal vein about one-third the length of the proximal portion (Fig. 31) (about equal in *M. dianthidii*) and the rim of the scutellum apically even in width and not projecting (apically widened and somewhat projecting in *M. dianthidii*). In females of *M. brevicrus* metasomal tergum 6 is obtuse in profile (as in Fig. 33) (acute in *M. dianthidii*, as in Fig. 32) The males of *M. brevicrus* are unique among New World males in modifications found in the fore leg and in the sunken lower face. In males the fore leg is reduced (Fig. 40) with the tibia shorter in length than the femur and ventrobasally concave, and the tarsomeres shortened with the claw length equal to tarsomeres 3 and 4 (fore leg unmodified in other species, cf. Fig. 39).

Monodontomerus clementi Grissell

Distribution.—NEARCTIC: Wyoming and Colorado, USA.

Hosts.—*Dianthidium heterulkei* (Megachilidae) [also reared from the factitious host *Megachile rotundata* (Megachilidae) in the laboratory].

Biology.—Clement (1976) found this species feeding on prepupae in cocoons of *D. heterulkei*. Goodpasture (1975) described the mating behavior, which is identical to that of *Monodontomerus montivagus*.

Discussion.—*Monodontomerus clementi* and *M. laticornis* are similar in having the anterior half of the upper mesepimeral area reticulately sculptured and the anterodorsal corner with diagonal striations extending nearly to transepimeral sulcus (Fig. 53). They differ in the characters outlined in couplet 11 of the key.

Monodontomerus dianthidii Gahan.

Distribution.—NEARCTIC: Eastern California and southwestern Oregon, USA.

Hosts.—*Dianthidium* sp. (Megachilidae).

Biology.—Reared from resin nests.

Discussion.—*Monodontomerus dianthidii* is phenetically most similar to *M. brevicrus*

based upon the completely sculptured frenal area and metasomal tergum 2; the differences between these species are discussed in detail under *M. brevicrus* above.

Monodontomerus laticornis Grissell and Zerova

Distribution.—PALEARCTIC: Russia, Kazakhstan, Ukraine, and Moldavia.

Hosts.—Reared from *Megachile rotundata* (Megachilidae); *Megachile centuncularis* and *Anthidium florentinum* (Zerova and Stolbov 1986) (Megachilidae); *Anthidium septemspinosum* (Zerova and Seryogina (2002). [A report of *Apis mellifera* as host (documented in Noyes 2003) seems unlikely].

Biology.—This is a gregarious parasitoid within cocoons of the hosts.

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the Former Soviet Union. This species and *M. clementi* are similar in appearance, and characters to distinguish them are given under couplet 11 of the key. *Monodontomerus laticornis* is a Palearctic species and *M. clementi* a Nearctic one, so they should not be readily confused.

Monodontomerus mandibularis Gahan

Distribution.—NEARCTIC: Widespread throughout the eastern USA and Canada from Saskatchewan south to Louisiana.

Hosts.—*Anthophora abrupta*, *A. bomboides bomboides*, *Melitoma taurea* (Apidae); *Osmia cordata* (Megachilidae) (Rau 1947).

Biology.—Rau (1947) published some preliminary information on the life history of this species, which he concluded had one or two generations per year. He believed the wasp to be a primary, gregarious parasitoid of its host.

Discussion.—*Monodontomerus mandibularis* is morphologically similar to *M. montivagus* but differs in both sexes (and from all other *Monodontomerus* species) by the mandibles having a single large, ventral tooth and a smaller, subapical dorsal one (Fig. 48). Other species have two ventral teeth and a small subapical dorsal one (as in Fig. 47) or have the dorsal tooth so reduced as to be easily overlooked. The mandibles are not generally exposed, however, so that for practical purposes *M. mandibularis* is best distinguished from *M. montivagus* as follows: In females the intermalar distance is about 3× the malar distance (about 2× in *M. montivagus*; this is the result of the malar distance being relatively shorter in *M. mandibularis* and the face less produced ventrally below the eyes, cf. Figs 47, 48) and the posterior outline of metasomal tergum 6 is deeply concave (shallow in *M. montivagus*, cf. Figs 32, 33); in males the scape (Fig. 57) is laterally compressed and distinctly C-shaped in profile with dorsal and ventral arches asymmetrical (in *M. montivagus* the scape is dorsoventrally compressed and nearly symmetrically curved in profile, Fig. 56, sometimes greatly so).

Monodontomerus mexicanus Gahan

Distribution.—NEARCTIC/NEOTROPICAL: Spotty distribution in Arizona, north-central Mexico, and western Panama.

Hosts.—*Megachile peruviana* (Megachilidae) (Rau 1947); *Ancyloscelis apiformis* (as *armata*) (Torchio 1974) and *Anthophora marginata* (Apidae) (Herting 1977).

Discussion.—This species has also been reared from *Trypoxylon mexicanum* (Gahan 1941), *T. monteverde*, and *Passaloecus* (= *Polemistus*) *pusillus* (Rau 1947) (all Crabronidae). It has been seen walking on the surface of *Trypoxylon* mud nests and drilling with its ovipositor through the mud walls (Brockmann in *litt.*). It is similar to *M. argentinus* and is discussed under that species.

Monodontomerus montivagus Ashmead

Distribution.—NEARCTIC: Widespread throughout southern Canada and USA. NEOTROPICAL: Southern Mexico (Guerrero).

Hosts.—This species has been reared from the following bees. Apidae: *Anthophora abrupta, Anthophora bomboides bomboides, Anthophora bomboides neomexicana, Anthophora linsleyi, ?Anthophora occidentalis, ?Anthophora vallorum, Bombus morrisoni, ?Melissoides* sp., *Xylocopa tabaniformis orpifex*. Megachilidae: *Anthidium collectum, Anthidium emarginatum, Anthidium ?mormonum, Anthidium* nest, *Ashmeadiella californica, Dianthidium curvatum sayi, Dianthidium pudicum pudicum, Dianthidium pudicum consimile, Hoplitis anthocopoides* nest, *Megachile centuncularis, Megachile relativa, Megachile rotundata, Osmia* sp. cocoon (in *Trypoxylon politum* nest [Crabronidae]), *Osmia cordata, Osmia kincaidii, Osmia latisulcata, Osmia lignaria, Osmia ribifloris, Osmia sanrafaelae, Osmia texana, Stelis depressa*.

Biology.—This is a gregarious, external parasitoid of aculeate Hymenoptera. Although there are numerous references to this species in the literature (see Peck 1963), most of these are simply host records without biological data. A few papers cited by Peck are of interest and are cited below. Davidson (1893: 153) stated that females of *M. montivagus* deposited 10 to 20 eggs in each cell of *Xylocopa tabaniformis orpifex* and that some broods were all males while others were all females. Hicks (1926: 224) stated that *M. montivagus* was parasitic both on *Anthophora occidentalis* and its parasitoid *Oryttus miraudus*, thus acting as a primary and secondary parasitoid. Mickel (1928: 72–73) reared 415 specimens, of which 94% were females, from 21 cells of *Anthophora occidentalis*. He found no hyperparasitic relationship on the same bee host as reported by Hicks (1926). Linsley and MacSwain (1942: 409–411) also reported *montivagus* as both a primary and a hyperparasitoid on *Anthophora linsleyi* and its mutillid parasitoid *Photopsis auraria* (now = *Sphaeropthalma unicolor*). These authors discussed the courtship behavior of *montivagus* and stated that its larvae fed on the prepupal stage of the bee. They stated that only one cell (of 9) had mixed sexes of this parasitoid, the others being either female (average 26 per cell) or male (average 40 per cell). In later rearings, however, MacSwain (1958: 395) found mixes of males and females in each of four cells of *A. occidentalis*. The sex ratio (males:females) varied from 1 to 12 to 1 to 30. Rau (1922) found a ratio of 1 to 6. Goodpasture (1975) described and illustrated the courtship behavior of *M. montivagus*. It is apparent from the literature and from reared specimens that *M. montivagus* is parasitic on bees, wasps, and their nest associates. New and old nests of aculeate Hymenoptera are complex sites of diverse taxa, behaviorial types, and successional faunas. Therefore, our biological knowledge of *M. montivagus* is almost wholly inadequate.

Morphology.—Goodpasture (1975) described and illustrated the male scapes and the haploid karyotype. This species has 6 chromosomes in males, 12 in females.

Discussion.—Females of *M. montivagus* are morphologically similar to other species reared from bees (e.g., *M. parkeri, M. tepedinoi, M. torchioi, M. mandibularis*), but males differ notably in morphology of the scape. The differences between *M. montivagus* and the others mentioned are discussed under each of these species.

Monodontomerus obscurus Westwood

Distribution.—NEARCTIC: Widespread from coast to coast in the United States and southeastern Canada. [Undoubtedly introduced into the Nearctic along with its host the alfalfa leafcutting bee.] PALEARCTIC: Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and probably often confused with *M. aeneus* which appears to be sympatric. The species is also reported from the oriental Region (India).

Hosts.—*Hoplitis* (as *Osmia*) *adunca, Megachile argentata, Megachile centuncularis, Megachile cephalotes, Megachile flavipes,*

Megachile lanata, *Megachile parietina* (as *Chalicodoma muraria*), *Megachile rotundata*, *M. willughbiella*, *Osmia cordata*, *Osmia cornifrons*, *Osmia latreillei*, *O. lignaria*, *Osmia ribfloris*, *Osmia rufa rufa*, *Osmia rufa cornigera*, *Osmia sanrafaelae*, (Megachilidae); *Anthophora plumipes*, *Xylocopa fenestrata* (Apidae).

Biology.—In Spain, *M. obscurus* is considered to be extremely destructive to the alfalfa leafcutting bee industry and chemical methods of control have been devised (Asensio 1982). Krunic and Radovic (1973) reported that *M. obscurus* can go through a number of generations without diapause and that diapause could be interrupted after keeping them for a time at 5°C.

Morphology.—Radu and Botoc (1968) illustrated female genitalia in detail. MacDonald and Krunic (1971) illustrated the somatic chromosomes for *M. obscurus*, which number 6 in males and 12 in females. (This differs from *M. aeneus* and thus strengthens the case for reproductive isolation between these two nearly identical species.) Baker et al. (1985) described and illustrated the last instar larva and pupa of this species (adult identity confirmed by examination of voucher specimens in North Carolina State University Insect Collection).

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the former Soviet Union. This species is similar to *M. aeneus* and is often reared from the same species of host in the same locality. I discuss the two species more fully under *M. aeneus*, above.

Monodontomerus osmiae Kamijo

Distribution.—PALEARCTIC: Known from Japan and the Russian Far East and introduced into the Nearctic (Grissell 2003).

Hosts.—*Osmia cornifrons*, *Osmia excavata*, and *Osmia taurus*, (Megachilidae) (Kamijo 1963, 1965).

Biology.—Iwata and Tachikawa (1966) reported a preponderance of females for rearings of this species from *Osmia taurus*. From 61 cocoons emerged 87 males and 726 females. The number of parasitoids per host (counted for 4 cocoons only) varied from 14 to 26.

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the former Soviet Union. Grissell (2003) illustrated the peculiar male head of this species based on specimens collected in Silver Spring, Montgomery County, Maryland, USA. *Monodontomerus japonicus* Ashmead was reported from *Osmia taurus*, but this record is undoubtedly a misidentification of *M. osmiae* (Grissell 1995). Males of this species are easily identified by the peculiar head (Figs 21, 22). Females have the discal area entirely setose.

Monodontomerus parkeri Grissell

Distribution.—NEARCTIC: Known from widespread localities in western North America stretching from Alberta, Canada to New Mexico, USA.

Host.—*Anthophora occidentalis* (Apidae).

Discussion.—*Monodontomerus parkeri* appears most similar to *M. tepedinoi* and their separation is discussed under the latter species. This species is also easily confused with *M. montivagus*. Males of the two species may be readily distinguished by comparing scapes: in *M. parkeri* the scape is laterally compressed and asymmetrically bent with the apex enlarged and a polished, depressed area on its outer side that continues onto the ventral surface (somewhat as in Fig. 57); in *M. montivagus* the scape is dorsoventrally compressed, symmetrically bent, and has the polished area completely ventral (Fig. 56). Additionally, in both sexes of *M. parkeri*, the apex of the costal cell dorsally has few setae (0 to 3 as in Fig. 43) whereas in *M. montivagus* there is a dorsal row of setae in the apical half to quarter (as in Fig. 31), and the transepim-

eral sulcus is complete (Fig. 54), whereas in *M. montivagus* it is not (Fig. 55). There are several less obvious and more relative characters that are difficult to use without comparative material. In *M. parkeri* the frenal area appears medially polished under reflected light even though it is sculptured, whereas in *M. montivagus* this area is generally entirely sculptured. In *M. parkeri* the admarginal wing area contains a few, widespaced setae (Fig. 44), and relatively few setae (3 to 5) are directly adjacent to the marginal vein (so that there is no setal row parallel to the vein), but in *M. montivagus* this area is evenly setose to the marginal vein (as in Fig. 43); there are enough setae to form a row parallel to the vein.

Monodontomerus rugulosus Thomson

Distribution.—PALEARCTIC: Widespread in western and central Europe (Zerova and Seryogina 2002).

Hosts.—This species has been reared from *Megachile rotundata* (Megachilidae) (Zerova and Romasenko 1986).

Biology.—This is a gregarious parasitoid in cocoons of its host.

Discussion.—*Monodontomerus rugulosus* appears quite similar to *M. argentinus*, but the two species occur in different, widely spaced zoogeographic regions. They may be separated by characters given in the key.

Monodontomerus tepedinoi Grissell

Distribution.—NEARCTIC: Known from Oregon and Utah, USA.

Hosts.—The species has been reared from *Osmia ligniaria* (Megachilidae).

Discussion.—Females of *M. tepedinoi* are easily confused with *M. montivagus* and *M. parkeri*. From *M. montivagus* it is most readily separated by the upper anterior margin of the costal cell with only 1 to 3 setae at the apex (as in Fig. 43), whereas in *M. montivagus* the upper anterior margin has a setal row in its apical 1/4 to 1/3 (as in Fig. 31). From *M. parkeri* it is separated by the longer ovipositor (ca. 1.5 to almost 2× the metasomal length; 1 to 1.2× in *M. parkeri*) and by the scape, which has some metallic green color at least ventrally (all yellow to orange in *M. parkeri*). Males of *M. tepedinoi* are easier to distinguish than females based on the antenna as described in the key and compared in Figs 56, 57, 58). *Monodontomerus tepedinoi* is so far associated only with Megachilidae and *M. parkeri* with Apidae.

Monodontomerus thorpi Grissell

Distribution.—NEARCTIC: Known from isolated localities in southern California, Arizona, and western Texas, USA.

Hosts.—Reared from nests of *Anthidium maculatum* (Megachilidae).

Discussion.—This species has been reared from twig nests in the eastern and western extremes of its distribution. It is one of the easiest species of the genus to identify in both sexes as it is the only species to have the first two flagellar segments reduced (i.e., ring-like, Fig. 19), whereas all other species have only the first segment reduced (Fig. 20). Additionally, the hind femur is enlarged with only a ventral angle (Fig. 36) as opposed to other species that have a distinct tooth (Figs 37, 38).

Monodontomerus torchioi Grissell

Distribution.—NEARCTIC: The species is known only from Utah, USA.

Hosts.—Reared from nests of *Osmia ligniaria* and *O. sanrafaelae* (Megachilidae).

Discussion.—*Monodontomerus torchioi* is easily confused with *M. montivagus*, *M. tepedioni*, and *M. parkeri* in females. The diagnostic characters used to separate these three taxa are given in key couplets 15 and 24–25 and under the discussion of the species mentioned.

Pseudotorymus Masi

Recognition.—Anterior margin of metapleuron straight (as in Fig. 2); occipital carina medially arched and midway be-

tween the hind ocelli and occipital foramen (as in Fig. 17); hind femur ventrally with a slight indication of a tooth; marginal vein long, 3 to 7× length of postmarginal vein and at least 6× length of stigmal vein.

Number of Species.—43.

Number Associated with Bees.—1 (questionably).

Distribution.—The genus is most abundant in the Palearctic Region (30 species) where its species are widespread and extend into northern Africa. It is also known from the Afrotropical Region (7 species) from Madagascar, Mali, Mozambique, Nigeria, Rwanda (Republic of the Congo), Senegal, South Africa, and Sudan. There are 4 species known from India in the Oriental Region and a single, widespread species is known from the Nearctic (southern Canada and northern USA).

Hosts.—Members have a broad host association including Curculionidae (Coleoptera) in leguminous seed pods; Bruchidae (Coleoptera) from galls on Asteraceae, Combretaceae, Fabaceae, Orchidaceae, and Rubiaceae; Cecidomyiidae (Diptera) associated with Apiaceae, Cruciferae, Fabaceae, Lamiaceae, Rosaceae, Salicaceae, and Scrophulariaceae; Eurytomidae (Hymenoptera) in grass stems (Poaceae); Cynipidae (Hymenoptera) in pods of Papaveraceae; Tenthredinidae (Hymenoptera); and Pyralidae (Lepidoptera).

Discussion.—The inclusion of this genus in relation to bee hosts is highly questionable and is based upon the single record for *P. indicus* as indicated below. Among the other 42 known species of *Pseudotorymus* the use of bees is unknown so this record is likely to be incorrect.

Pseudotorymus indicus (Mani)

Distribution.—This species is known only from southern India (Uttar Pradesh, Tamil Nadu) (Mani 1989).

Hosts.—The type series was reared from "flower bud galls" on *Dalbergia sissoo* (Fabaceae). Mani (1989) listed the host as a "leafcutting bee".

Discussion.—In light of the original rearing and the entire host range given above, I am inclined to dismiss this record until it can be reconfirmed.

Torymus Walker

Recognition.—This genus is easily recognized by the anterior edge of the metapleuron (usually its upper half) projecting forward as a lobe into the mesepimeron which is subdivided into upper and lower sections, the lower of which is delimited by an anterior groove (Fig. 1, compare with Fig. 2, arrows).

Number of Species.—Approximately 375.

Number Associated with Bees.—3.

Distribution.—All zoogeographic regions except Australia where it was apparently introduced (Grissell 1995).

Hosts of Genus.—Members of this genus are mostly parasitoids of larvae of gall-forming Diptera and Hymenoptera. A few have been reared from bees, and a few are phytophagous in seeds.

Discussion.—Until 1998 the species that parasitized bees were treated as the genus *Diomorus* Walker. Graham and Gijswijt (1998) synonymized *Diomorus* under *Torymus*, dividing its members into several species groups of the latter.

Torymus armatus (Boheman)

Distribution.—This species is widespread in the Palearctic, being reported from Europe (Graham and Gijswijt 1998) and Japan (Kamijo 1979). It was possibly introduced into Papua New Guinea (Bouček 1988).

Hosts.—Kamijo (1979) reported *T. armatus* from *Ceratina japonica* (Apidae) in *Rubus* twigs (Rosaceae) in Japan.

Discussion.—This species has reportedly been reared from several genera of Crabronidae, including *Rhopalum* (Box 1920) and *Crossocerus* (Gijswijt 1974), and seems to be associated with wasps and bees that

nest in the stems of *Rubus* (Graham and Gijswijt 1998). It is the most distinct of the three *Torymus* species known from bees, having the hind coxa dorsally bare and smooth, and the propodeum without carinae.

Toymus cupreus (Spinola)

Distribution.—The species is widespread in the Palearctic (Nikol'skaya and Zerova 1978), mostly in the "southern parts and middle of Europe" and reaching into the Netherlands (Graham and Gijswijt 1998). It is reported from Burma in the Oriental Region (Mani and Kaul 1972).

Host.—The original hosts given by Spinola included 7 species of cynipid galls, but these all probably housed aculeate bees or wasps. Mani and Kaul (1972) reported the species as "widely distributed as [a] parasitoid of *Osmia* sp. (Megachilidae) and Sphecidae."

Biology.—Enslin (1922) illustrated and discussed the larval and pupal stages of this species (as *Diomorus kollari*).

Discussion.—This Palearctic species and the following Nearctic species are geographically separated but show no morphological differences. In coloration, however, they are distinct as explained in key couplet 3.

Torymus zabriskii (Cresson)

Distribution.—The species is widespread in the United States.

Hosts.—The only reported bee host is *Ceratina dupla* (Apidae) (Zabriskei 1890).

Biology.—Krombein (1964) reported some short biological notes on this species (as *Diomorus*) as a parasitoid of *Ectemnius paucimaculatus* (Crabronidae). He suggested that *T. zabriskii* parasitized several cells in a succession of cells and that oviposition was probably through the wall of the plant stem (*Hibiscus*: Malvaceae) in which the wasp nested.

Discussion.—*Ceratina*, the only reported bee host (Zabriskei 1890), has been listed in the secondary literature several times but has never been reconfirmed. A number of other hosts in the family Crabronidae have been reported for this species including *Ectemnius*, *Crossocerus*, and *Rhopalum* (summarized by Grissell 1995).

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APPENDIX

Two lists are presented: bee host/chalcidoid and chalcidoid/bee host. The bee host list presents names as they currently are applied in the literature (i.e., valid names), not as they were originally published. The lists are derived from Bouček (1974), Noyes (2003), and Grissell (1995, 2000, 2005). Authors' names are given for bee host in the first list; chalcidoid authors are given in the subsequent list. The placement of bee genera in families is based on an electronic version (http://faculty.ucr.edu/~heraty/beepage.html) of Michener (2000).

Bee Host/Chalcidoid

Apidae

Allodape exoloma Strand: *Xylencyrtus tridens*

Allodape mucronata Smith: *Xylencyrtus tridens*

Allodape panurgoides Smith: *Xylencyrtus tridens*

Allodape rufogastra Lepeletier and Serville: *Xylencyrtus tridens*

Allodapula grandiceps (Friese): *Xylencyrtus tridens*

Allodapula melanopus (Cameron): *Xylencyrtus mumifex*

Ancyloscelis apiformis (F.): *Monodontomerus mexicanus*

Anthophora abrupta Say: *Melittobia acasta*, *Melittobia megachilis*, *Pediobius williamsoni*, *Monodontomerus mandibularis*, *Monodontomerus montivagus*

Anthophora bomboides bomboides Kirby: *Leucospis gigas*, *Monodontomerus mandibularis*, *Monodontomerus montivagus*

Anthophora bomboides neomexicana Cockerell: *Monodontomerus montivagus*

Anthophora linsleyi Timberlake: *Monodontomerus montivagus*

Anthophora marginata Smith: *Monodontomerus mexicanus*

Anthophora occidentalis Cresson: *Monodontomerus montivagus*, *Monodontomerus parkeri*

Anthophora plumipes (Pallas): *Monodontomerus obscurus*

Anthophora retusa (L.): *Melittobia acasta, Melittobia pelopoei, Monodontomerus aeneus*
?Anthophora vallorum (Cockerell): *Monodontomerus montivagus*
Apis cerana (F.): *Antrocephalus* sp.
Apis mellifera L.: *Dibrachys boarmiae, Melittobia acasta, Monodontomerus laticornis, Nasonia vitripennis, Pteromalus apum, Tetrastichus howardi*
Bombus agrorum F.: *Pteromalus conopidarum*
Bombus americanorum F.: *Pediobius williamsoni*
Bombus atratus Franklin: *Pediobius williamsoni*
Bombus fervidus F.: *Melittobia chalybii*
Bombus hortorum (L.): *Melittobia acasta*
Bombus lapidarius (L.): *Pteromalus conopidarum*
Bombus morrisoni Cresson: *Monodontomerus montivagus*
Bombus ruderatus (F.): *Melittobia acasta*
Bombus sp.: *Dibrachys cavus, Melittobia hawaiiensis, Pachycrepoideus vindemmiae*
Bombus terrestris (L.): *Melittobia acasta*
Braunsapis leptozonia (Vachal): *Xylencyrtus tridens*
Braunsapis rolini (Vachal): *Echthrodape africana*
Braunsapis rufipes (Friese): *Echthrodape africana*
Braunsapis simplicipes Michener: *Echthrodape africana*
Braunsapis unicolor Smith: *Echthrodape papuana*
Centris analis F.: *Leucospis cayennensis*
Centris bicornuta Mocsary: *Leucospis cayennensis*
Centris nitida Smith: *Leucospis cayennensis*
Centris tarsata (Smith): *Leucospis cayennensis*
Centris vittata Lepeletier: *Leucospis cayennensis*
Ceratina calcarata Robertson: *Axima zabriskiei*
Ceratina callosa (F.): *Eurytoma nodularis, Monodontomerus aeneus*
Ceratina dallatorreana Friese: *Eurytoma apiculae*
Ceratina dupla Say: *Axima zabriskiei, Baryscapus americanus, Habritys latrus, Torymus zabriskii*
Ceratina flavipes Smith: *Neochalcis breviceps*
Ceratina ignara Cresson: *Baryscapus americanus*
Ceratina japonica Cockerell: *Cleonymus ceratinae, Torymus armatus*
Ceratina nanula Cockerell: *Baryscapus americanus, Eurytoma apiculae*
Ceratina punctigena Cockerell: *Eurytoma apiculae*
Ceratina sequoiae Michener: *Baryscapus americanus*
Ceratina sp.: *Cheiloneurus leptulus, Epistenia coeruleata, Melittobia megachilis, Micrapion dalyi, Micrapion nasutum, Micrapion richardsi*
Ceratina truncata Friese: *Micrapion steffani*
?Ctenoplectra chalybea Smith: *Leucospis histrio*
Diadasina distincta (Holmberg): *Leucospis genalis*
Eufriesea nigrescens (Friese): *Monodontomerus argentinus*
Euglossa annectans Dressler: *Melittobia* sp.
Euglossa ignita Smith: *Polistomorpha fasciata*
Euglossa sp.: *Polistomorpha conura, Polistomorpha fasciata*
Eulaema meriana (Oliver): *Leucospis pinna*
?Melissodes sp.: *Monodontomerus montivagus*
Melitoma taurea (Say): *Monodontomerus mandibularis*
Trigona sp.: *Brachymeria discreta*
Xylocopa brasilianorum (L.): *Leucospis klugii*
Xylocopa caerulea (F.): *Coelopencyrtus pallidiceps*
Xylocopa caffra (L.): *Coelopencyrtus callainus, Coelopencyrtus taylori*
Xylocopa divisa Klug: *Coelopencyrtus callainus, Coelopencyrtus taylori*
Xylocopa fenestrata (F.): *Monodontomerus obscurus*
Xylocopa flavicollis (De Geer): *Coelopencyrtus callainus*
Xylocopa flavorufa (De Geer): *Coelopencyrtus callainus, Coelopencyrtus taylori, Coelopencyrtus watmoughi*
Xylocopa frontalis (Oliver): *Coelopencyrtus gargaris*
Xylocopa inconstans Smith: *Coelopencyrtus callainus*
Xylocopa nogueirai Hurd and Moure: *Leucospis xylocopae*
Xylocopa pubescens Spinola: *Coelopencyrtus* sp.
Xylocopa scioensis Gribodo: *Coelopencyrtus cyprius*
Xylocopa sp.: *Leucospis reversa*
Xylocopa submordax Cockerell: *Leucospis anthidioides*
Xylocopa sulcatipes Maa: *Coelopencyrtus* sp.
Xylocopa tabaniformis orpifex Smith: *Monodontomerus montivagus*
Xylocopa tenuiscapa Westwood: *Coelopencyrtus krishnamurtii*
Xylocopa tranquebarorum (Swederus): *Melittobia sosui*
Xylocopa turanica Morawitz: *Melittobia acasta*
Xylocopa watmoughi Eardly: *Coelopencyrtus* sp.

Colletidae

Hylaeus communis Nylander: *Coelopencyrtus arenarius, Coelopencyrtus callidii*
Hylaeus cressoni Cockerell: *Coelopencyrtus hylaei*
Hylaeus ellipticus (Kirby): *Coelopencyrtus hylaeoleter*
Hylaeus fuscipennis (Smith): *Coelopencyrtus kaalae*

Hylaeus heraldicus (Smith): *Coelopencyrtus nothylaei*
Hylaeus koae (Perkins): *Coelopencyrtus kaalae*
Hylaeus nigritus (F.): *Coelopencyrtus arenarius*
Hylaeus polifolii Cockerell: *Eurytoma stigmi*
Hylaeus pubescens (Perkins): *Coelopencyrtus kaalae, Coelopencyrtus sexramosus*
Hylaeus sp.: *Eurytoma nodularis, Melittobia acasta, Melittobia hawaiiensis*
Hylaeus varifrons Cresson: *Pteromalus analis*

Halictidae

Halictus africanus Friese: *Aperilampus varians*
?*Lasioglossum pruinosum* (Robertson): *Eupelmus ashmeadi, Eupelmus rhizophelus*
Nomia melanderi Cockerell: *Mesopolobus bruchophagi*

Megachilidae

Anthidiellum perplexum Smith: *Leucospis affinis*
Anthidiellum sp.: *Leucospis slossonae*
Anthidiellum strigatum (Panzer): *Leucospis bifasciata, Leucospis dorsigera*
Anthidium collectum Huard: *Monodontomerus montivagus*
Anthidium diadema Latreille: *Leucospis dorsigera*
Anthidium emarginatum (Say): *Leucospis affinis, Leucospis dorsigera, Monodontomerus montivagus*
Anthidium florentinum (F.): *Melittobia acasta, Monodontomerus aeneus, Monodontomerus laticornis*
Anthidium maculatum Smith: *Monodontomerus thorpi*
Anthidium maculosum Cresson: *Leucospis affinis*
Anthidium ?*mormonum* Cresson: *Monodontomerus montivagus*
Anthidium septemspinosum Lepeletier: *Monodontomerus laticornis*
Ashmeadiella aridula astragali Michener: *Leucospis affinis*
Ashmeadiella bigeloviae (Cockerell): *Microdontomerus parkeri*
Ashmeadiella californica (Ashmead): *Monodontomerus montivagus*
Ashmeadiella cubiceps (Cresson): *Microdontomerus parkeri*
Ashmeadiella gillettei Titus: *Microdontomerus parkeri*
Ashmeadiella meliloti Cockerell: *Leucospis affinis*
Ashmeadiella rufipes Titus: *Microdontomerus parkeri*
Coelioxys octodentata Say: *Aprostocetus* sp., *Merisus* sp., *Tetrastichus coelioxydis*
?*Coelioxys quadridentatus* (L.): *Leucospis gigas*
Dianthidium curvatum sayi Cockerell: *Monodontomerus montivagus*
Dianthidium heterulkei Schwarz: *Monodontomerus clementi*
Dianthidium pudicum pudicum (Cresson): *Leucospis affinis, Monodontomerus montivagus*
Dianthidium pudicum consimile (Ashmead): *Microdontomerus anthidii, Monodontomerus montivagus*
Dianthidium sp.: *Monodontomerus dianthidii*
Heriades crenulatus Nylander: *Eurytoma heriadi, Melittobia acasta*
?*Heriades* sp.: *Leucospis dorsigera*
Heriades truncorum (L.): *Melittobia acasta*
Hoplitis acuticornis (Dufour and Perris): *Leucospis biguetina*
Hoplitis adunca (Panzer): *Eurytoma nodularis, Leucospis dorsigera, Melittobia acasta, Monodontomerus aeneus, Monodontomerus obscurus*
Hoplitis anthocopoides (Schenck) (nest): *Monodontomerus montivagus*
Hoplitis bullifacies Michener: *Microdontomerus enigma, Microdontomerus parkeri*
Hoplitis palmarum (Cockerell): *Microdontomerus parkeri*
Hoplitis producta (Cresson): *Cleonymus amabilis, Eurytoma amplicoxa, Eurytoma stigmi, Leucospis affinis*
Hoplitis tridentata (Dufour and Perris): *Leucospis biguetina, Neochalcis osmicida*
Hoplosmia ligurica (Morawitz): *Leucospis dorsigera*
Lithurgus capensis Friese: *Leucospis ornata, Leucospis varicollis*
Megachile aetheria Mitchell: *Melittobia hawaiiensis*
Megachile albitarsis Cresson: *Ablaxia cupraeus*
Megachile apicalis Spinola: *Monodontomerus aeneus*
Megachile argentata (F.): *Dibrachys cavus, Melittobia acasta, Monodontomerus obscurus*
Megachile bombycina Radoszkowski: *Melittobia acasta*
Megachile brevis Say: *Aprostocetus* sp., *Cricellius megachilis, Leucospis affinis, Melittobia chalybii, Merisus* sp., *Microdontomerus parkeri, Tetrastichus coelioxydis*
Megachile centuncularis (L.): *Ablaxia cupraeus, Anagrus putnamii, Aprostocetus pygmaeus, Baryscapus megachilidis, Dibrachys* sp., *Melittobia acasta, Melittobia chalybii, Melittobia megachilis,*

Monodontomerus aeneus, Monodontomerus laticornis, Monodontomerus montivagus, Monodontomerus obscurus, Pteromalus apum, Pteromalus macronychivorus

Megachile cephalotes Smith: *Monodontomerus obscurus*

Megachile concinna Smith: *Baryscapus megachilidis, Melittobia australica, Monodontomerus aeneus*

Megachile disjunctiformis Cockerell: *Leucospis japonica*

Megachile ericetorum Lepeletier: *Leucospis dorsigera*

Megachile flavipes Spinola: *Monodontomerus obscurus*

Megachile gentilis Cresson: *Baryscapus megachilidis, Leucospis affinis*

Megachile gomphrenae Holmberg: *Melittobia hawaiiensis*

Megachile gratiosa Cameron: *Melittobia* sp.

Megachile hungarica Gerstaecker: *Leucospis gigas*

Megachile inermis Provancher: *Leucospis affinis, Melittobia chalybii*

Megachile lanata (F.): *Melittobia australica, Monodontomerus obscurus*

Megachile mendica Cresson: *Leucospis affinis*

Megachile montivaga Cresson: *Leucospis affinis, Microdontomerus apianus*

Megachile nipponica Cockerell: *Leucospis japonica*

Megachile pallefacta Vachal: *Melittobia hawaiiensis*

Megachile palmarum Perkins: *Melittobia hawaiiensis*

Megachile parietina (Geoffrey): *Leucospis gigas, Melittobia acasta, Monodontomerus aeneus, Monodontomerus obscurus*

Megachile peruviana Smith: *Monodontomerus mexicanus*

Megachile poeyi Guérin-Méneville: *Leucospis poeyi*

Megachile pugnata Say: *Dibrachys* sp., *Leucospis affinis, Melittobia* sp., *Monodontomerus bakeri*

Megachile pyrenaica Lepeletier: *Leucospis gigas, Pteromalus apum*

Megachile rancaguensis Friese: *Leucospis hopei*

Megachile rangii Cheesman: *Leucospis aruina*

Megachile relativa Cresson: *Dibrachys relativus, Leucospis affinis, Melittobia acasta, Melittobia chalybii, Monodontomerus bakeri, Monodontomerus montivagus, Pteromalus apum*

Megachile rotundata (F.): *Baryscapus daira, Baryscapus megachilidis, Dibrachys confusus, Dibrachys maculipennis, Melittobia acasta, Melittobia australica, Melittobia chalybii, Melittobia hawaiiensis, Monodontomerus aeneus, Monodontomerus bakeri, Monodontomerus clementi* (in lab), *Monodontomerus laticornis, Monodontomerus montivagus, Monodontomerus obscurus, Monodontomerus rugulosus, Pteromalus apum, Pteromalus conopidarum, Pteromalus veneris, Tetrastichus* sp.

Megachile sculpturalis Smith: *Leucospis japonica*

Megachile sicula Rossi: *Leucospis gigas, Monodontomerus aeneus*

Megachile sp.: *Brachymeria paraguayensis, Calosota fumipennis, Horismenus albipes, Kocourekia clavigera, Leucospis histrio, Leucospis intermedia, Melittobia pelopoei, Monodontomerus acrostigmus, Monodontomerus argentinus*

Megachile spissula (Cockerell): *Lariophagus obtusus, Melittobia acasta*

Megachile ustulatum (Smith): *Leucospis histrio*

Megachile willowmorensis Brauns: *Leucospis ornata*

Megachile willughbiella (Kirby): *Melittobia acasta, Monodontomerus obscurus, Pteromalus apum*

Megachile xylocopoides Smith: *Baryscapus megachilidis*

Megachile zaptlana Cresson: *Melittobia australica*

Microthurge corumbae (Cockerell): *Leucospis* sp.

Osmia atriventris Cresson: *Leucospis affinis*

Osmia bicolor (Schrank): *Eulophus osmiarum*

Osmia bicornis (Schrank): *Leucospis dorsigera, Leucospis gigas*

Osmia brevicornis (F.): *Monodontomerus aeneus*

Osmia californica Cresson: *Leucospis affinis*

Osmia "coerulea" [?*lapsus* for *O. coerulescens*, Baur and Amiet 2000]: *Leucospis gigas*

Osmia coerulescens (L.): *Aprostocetus pygmaeus, Eurytoma nodularis, Leucospis gigas, Monodontomerus aeneus*

Osmia coloradensis Cresson: *Monodontomerus bakeri*

Osmia cordata Robertson: *Monodontomerus mandibularis, Monodontomerus montivagus, Monodontomerus obscurus*

Osmia cornifrons Radoszkowski: *Monodontomerus obscurus, Monodontomerus osmiae*

Osmia cornuta (Latreille): *Leucospis dorsigera, Monodontomerus aeneus*

Osmia emarginata Lepeletier: *Leucospis intermedia, Monodontomerus aeneus*

Osmia excavata Alfken: *Leucospis japonica, Monodontomerus osmiae*

Osmia fedtschenkoi (Morawitz): *Leucospis dorsigera*

Osmia fulviventris (Panzer): *Leucospis dorsigera, Monodontomerus aeneus*

Osmia globicola (Stadelmann): *Leucospis osmiae*

Osmia kincaidii Cockerell: *Leucospis affinis, Monodontomerus montivagus*
Osmia latisulcata Michener: *Monodontomerus montivagus*
Osmia latreillei (Spinola): *Calosota vernalis, Monodontomerus aeneus, Monodontomerus obscurus*
Osmia leucomelana (Kirby): Eurytoma sp., Melittobia acasta
Osmia lignaria Say: *Monodontomerus montivagus, Monodontomerus obscurus, Monodontomerus tepedinoi, Monodontomerus torchioi*
Osmia marginata Michener: *Microdontomerus parkeri*
Osmia nigrifrons Cresson: *Dibrachys pelos, Monodontomerus aeneus*
Osmia niveata (F.): *Leucospis dorsigera*
Osmia parietina Curtis: *Leucospis dorsigera*
Osmia parvula Dufour and Perris: *Eurytoma nodularis*
Osmia pumila Cresson: *Leucospis affinis*
Osmia ribifloris Cockerell: *Monodontomerus brevicrus, Monodontomerus montivagus, Monodontomerus obscurus*
Osmia rostrata Sandhouse: *Leucospis affinis*
Osmia rufa cornigera (Rossi): *Monodontomerus aeneus, Monodontomerus obscurus*
Osmia rufa rufa (L): *Leucospis dorsigera, Leucospis gigas, Melittobia acasta, Monodontomerus aeneus, Monodontomerus obscurus*
Osmia sanrafaelae Parker: *Monodontomerus montivagus, Monodontomerus obscurus, Monodontomerus torchioi*
Osmia simillima Smith: *Leucospis affinis*
Osmia sp.: *Epistenia coeruleata, Monodontomerus montivagus* (cocoon in *Trypargilum politum* nest), *Torymus cupreus*
Osmia submicans Morawitz: *Monodontomerus aeneus*
Osmia taurus Smith: *Leucospis japonica, Monodontomerus osmiae*
Osmia texana Cresson: *Monodontomerus bakeri, Monodontomerus montivagus*
Osmia tricornis Latreille: *Leucospis dorsigera, Monodontomerus aeneus*
Pachyanthidium cordatum (Smith): *Leucospis tricolor*
Pachyanthidium truncataum (Smith): *Leucospis tricolor*
Pseudoanthidium lituratum (Panzer): *Adontomerus gregalis, Adontomerus nesterovi, Neochalcis fertoni*
Rhodanthidium sticticum (F.): *Monodontomerus anthidiorum*
Serapista denticulata (Smith): *Leucospis africana, Leucospis tricolor*
Stelis depressa Timberlake: *Monodontomerus montivagus*
Stelis nasuta Latreille: *Melittobia acasta, Monodontomerus aeneus*
Stelis sexmaculata Ashmead: *Cleonymus amabilis, Leucospis affinis*

Chalcidoid/Bee Host

Chalcididae

Antrocephalus sp.: *Apis cerana*
Brachymeria discreta Gahan: *Trigona* sp.
Brachymeria paraguayensis Girault: *Megachile* sp.
Neochalcis breviceps (Masi): *Ceratina flavipes*
Neochalcis fertoni (Kieffer): *Pseudoanthidium lituratum*
Neochalcis osmicida (Saunders): *Hoplitis tridentata*

Encyrtidae

Cheiloneurus leptulus Annecke and Prinsloo: *Ceratina* sp.
Coelopencyrtus arenarius (Erdös): *Hylaeus communis, Hylaeus nigritus*
Coelopencyrtus callainus Annecke: *Xylocopa caffra, Xylocopa divisa, Xylocopa flavicollis, Xylocopa flavorufa, Xylocopa inconstans*
Coelopencyrtus callidii (Jansson): *Hylaeus communis*
Coelopencyrtus cyprius Annecke: *Xylocopa scioensis*
Coelopencyrtus gargaris (Walker): *Xylocopa frontalis*
Coelopencyrtus hylaei Burks: *Hylaeus cressoni*
Coelopencyrtus hylaeoleter Burks: *Hylaeus ellipticus*
Coelopencyrtus kaalae (Ashmead): *Hylaeus fuscipennis, Hylaeus koae, Hylaeus pubescens*
Coelopencyrtus krishnamurtii (Mahdihassan): *Xylocopa tenuiscapa*
Coelopencyrtus nothylaei Annecke: *Hylaeus heraldicus*
Coelopencyrtus pallidiceps (Girault): *Xylocopa caerulea*
Coelopencyrtus sexramosus Timberlake: *Hylaeus pubescens*
Coelopencyrtus sp.: *Xylocopa pubescens, Xylocopa sulcatipes, Xylocopa watmoughi*
Coelopencyrtus taylori Annecke and Doutt: *Xylocopa caffra, Xylocopa divisa, Xylocopa flavorufa*

Coelopencyrtus watmoughi Annecke: *Xylocopa flavorufa*

Eulophidae

Aprostocetus pygmaeus Zetterstedt: *Megachile centuncularis, Osmia coerulescens*
Aprostocetus sp.: *Coelioxys octodentata, Megachile brevis*
Baryscapus americanus (Ashmead): *Ceratina dupla, Ceratina iguana, Ceratina nanula, Ceratina sequoiae*
Baryscapus daira (Walker): *Megachile rotundata*
Baryscapus megachilidis (Burks): *Megachile centuncularis, Megachile concinna, Megachile gentilis, Megachile rotundata, Megachile xylocopoides*
Eulophus osmiarum Robineau-Desvoidy: *Osmia bicolor*
Horismenus albipes (Schrottky): *Megachile* sp.
Kocourekia clavigera Bouček: *Megachile* sp.
Melittobia acasta (Walker): *Anthidium florentinum, Anthophora abrupta, Anthophora retusa, Apis mellifera, Bombus hortorum, Bombus ruderatus, Bombus terrestris, Heriades crenulatus, Heriades truncorum, Hoplitis adunca, Hylaeus* sp., *Megachile argentata, Megachile bombycina, Megachile centuncularis, Megachile parietina, Megachile relativa, Megachile rotundata, Megachile spissula, Megachile willughbiella, Osmia leucomelana, Osmia rufa, Stelis nasuta, Xylocopa turanica*
Melittobia australica Girault: *Megachile concinna, Megachile lanata, Megachile rotundata, Megachile zaptlana*
Melittobia chalybii Ashmead: *Bombus fervidus, Megachile brevis, Megachile centuncularis, Megachile inermis, Megachile relativa, Megachile rotundata*
Melittobia hawaiiensis Perkins: *Bombus* sp., *Hylaeus* sp., *Megachile aetheria, Megachile gomphrenae, Megachile pallefacta, Megachile palmarum, Megachile rotundata*
Melittobia megachilis (Packard): *Anthophora abrupta, Ceratina* sp., *Megachile centuncularis*
Melittobia pelopoei [unavailable name]: *Anthophora retusa, Megachile* sp.
Melittobia sosui Dahms: *Xylocopa tranquebarorum*
Melittobia sp.: *Euglossa annectans, Megachile gratiosa, Megachile puguata*
Pediobius williamsoni Girault: *Anthophora abrupta, Bombus americanorum, Bombus atratus*
Tetrastichus coelioxydis (Burks): *Coelioxys octodentata, Megachile brevis*
Tetrastichus howardi (Olliff): *Apis mellifera*
Tetrastichus sp.: *Megachile rotundata*
Torymus armatus (Boheman): *Ceratina japonica*
Torymus cupreus (Spinola): *Osmia* sp.
Torymus zabriskii (Cresson): *Ceratina dupla*
Xylencyrtus mumifex Annecke: *Allodapula melanopus*
Xylencyrtus tridens Annecke: *Allodape exoloma, Allodape mucronata, Allodape panurgoides, Allodape rufogastra, Allodapula grandiceps, Braunsapis leptozonia*

Eupelmidae

Calosota fumipennis Curtis: *Megachile* sp.
Calosota vernalis Curtis: *Osmia latreillei*
Eupelmus ashmeadi Melander and Brues: ?*Lasioglossum pruinosum*
Eupelmus rhizophelus Brues: ?*Lasioglossum pruinosum*

Eurytomidae

Axima zabriskiei Howard: *Ceratina calcarata, Ceratina dupla*
Eurytoma amplicoxa Bugbee: *Hoplitis producta*
Eurytoma apiculae Bugbee: *Ceratina dallatorreana, Ceratina nanula, Ceratina punctigena*
Eurytoma heriadi Zerova: *Heriades crenulatus*
Eurytoma nodularis Boheman: *Ceratina callosa, Hylaeus* sp., *Osmia adunca, Osmia coerulescens, Osmia parvula,*
Eurytoma sp.: *Osmia leucomelana*
Eurytoma stigmi Ashmead: *Hoplitis producta, Hylaeus polifolii*

Leucospidae

Leucospis affinis Say: *Anthidiellum perplexum, Anthidium emarginatum, Anthidium maculosum, Ashmeadiella aridula astragli, Ashmeadiella meliloti, Dianthidium pudicum, Hoplitis producta, Megachile brevis, Megachile gentilis, Megachile inermis, Megachile mendica, Megachile montivaga, Megachile pugnata, Megachile relativa, Osmia atriventris, Osmia californica, Osmia kincaidii, Osmia pumila, Osmia rostrata, Osmia simillima, Stelis sexmaculata.*
Leucospis africana Cameron: *Serapista denticulata*
Leucospis anthidioides Westwood: *Xylocopa submordax*
Leucospis aruina Walker: *Megachile rangii*
Leucospis bifasciata Klug: *Anthidiellum strigatum*
Leucospis biguetina Jurine: *Hoplitis acuticornis, Hoplitis tridentata*

Leucospis cayennensis Westwood: *Centris analis, Centris bicornuta, Centris nitida, Centris tarsata, Centris vittata*
Leucospis dorsigera F.: *Anthidiellum strigatum, Anthidium diadema, Anthidium emarginatum, ?Heriades* sp., *Hoplitis adunca, Hoplosmia ligurica, Megachile ericetorum, Osmia bicornis, Osmia cornuta, Osmia fedtschenkoi, Osmia fulviventris, Osmia niveata, Osmia parietina, Osmia rufa rufa, Osmia tricornis*
Leucospis genalis Bouček: *Diadasina distincta*
Leucospis gigas F.: *Anthophora bomboides bomboides, ?Coelioxys quadridentatus, Megachile hungarica, Megachile parietina, Megachile pyrenaica, Megachile sicula, Osmia bicornis, Osmia ?coerulescens, Osmia rufa rufa*
Leucospis histrio Maindron: *?Ctenoplectra chalybea, Megachile ustulatum*
Leucospis hopei Westwood: *Megachile rancaguensis*
Leucospis intermedia Illiger: *Megachile* sp., *Osmia emarginata*
Leucospis japonica Walker: *Megachile disjunctiformis, Megachile nipponica, Megachile sculpturalis, Osmia excavata, Osmia taurus*
Leucospis klugii Westwood: *Xylocopa brasilianorum*
Leucospis ornata Westwood: *Lithurgus capensis, Megachile willowmorensis*
Leucospis osmaie Bouček: *Osmia globicola*
Leucospis pinna Grissell and Cameron: *Eulaema meriana*
Leucospis poeyi Guérin-Méneville: *Megachile poeyi*
Leucospis reversa Bouček: *Xylocopa* sp.
Leucospis slossonae Weld: *Anthidiellum* sp.
Leucospis sp.: *Microthurge corumbae*
Leucospis tricolor Kirby: *Pachyanthidium cordatum, Pachyanthidium truncatum, Serapista denticulata*
Leucospis varicollis Cameron: *Lithurgus capensis*
Leucospis xylocopae Burks: *Xylocopa nogueirai*
Micrapion dalyi Bouček: *Ceratina* sp.
Micrapion nasutum Bouček: *Ceratina* sp.
Micrapion richardsi Bouček: *Ceratina* sp.
Micrapion steffani Bouček: *Ceratina truncata*
Polistomorpha conura Bouček: *Euglossa* sp.
Polistomorpha fasciata Westwood: *Euglossa ignita, Euglossa* sp.

Mymaridae

Anagrus putnamii Packard: *Megachile centuncularis*

Perilampidae

Aperilampus varians Strand: *Halictus africanus*

Pteromalidae

Ablaxia cupraeus (Provancher): *Megachile albitarsis, Megachile centuncularis*
Cleonymus amabilis Cockerell: *Hoplitis producta, Stelis sexmaculata*
Cleonymus ceratinae Kamijo: *Ceratina japonica*
Cricellius megachilis Ashmead: *Megachile brevis*
Dibrachys boarmiae (Walker): *Apis mellifera*
Dibrachys cavus (Walker): *Bombus* sp., *Megachile argentata*
Dibrachys confusus (Girault): *Megachile rotundata*
Dibrachys maculipennis Szelenyi: *Megachile rotundata*
Dibrachys pelos Grissell: *Osmia nigrifrons*
Dibrachys relativus Doganlar: *Megachile relativus*
Dibrachys sp.: *Megachile centuncularis, Megachile pugnata*
Epistenia coeruleata Westwood: *Ceratina* sp., *Osmia* sp.
Habritys latrus Wallace: *Ceratina dupla*
Lariophagus obtusus Kamijo: *Megachile spissula*
Merisus sp.: *Coelioxys octodentata, Megachile brevis*
Mesopolobus bruchophagi (Gahan): *Nomia melanderi*
Nasonia vitripennis (Walker): *Apis mellifera*
Pachycrepoideus vindemmiae Rondani: *Bombus* sp.
Pteromalus analis Ashmead: *Hylaeus varifrons*
Pteromalus apum (Retzius): *Apis mellifera, Megachile centuncularis, Megachile pyrenaica, Megachile relativa, Megachile rotundata, Megachile willughbiella*
Pteromalus conopidarum (Bouček): *Bombus agrorum, Bombus lapidarius, Megachile rotundata*
Pteromalus macronychivorus Perez: *Megachile centuncularis*
Pteromalus veneris Dalla Torre: *Megachile rotundata*

Torymidae

Adontomerus gregalis (Steffan): *Pseudoanthidium lituratum*
Adontomerus nesterovi Zerova: *Pseudoanthidium lituratum*
Echthrodape africana Burks: *Braunsapis rolini, Braunsapis rufipes, Braunsapis simplicipes*
Echthrodape papuana Bouček: *Braunsapis unicolor*

Microdontomerus anthidii (Ashmead): *Dianthidium pudicum consimile*

Microdontomerus apianus Grissell: *Megachile montivaga*

Microdontomerus enigma Grissell: *Hoplitis bullifacies*

Microdontomerus parkeri Grissell: *Ashmeadiella bigeloviae, Ashmeadiella cubiceps, Ashmeadiella gillettei, Ashmeadiella rufipes, Hoplitis bullifacies, Hoplitis palmarum, Megachile brevis, Osmia marginata*

Monodontomerus acrostigmus Grissell: *Megachile* sp.

Monodontomerus aeneus (F.): *Anthidium florentinum, Anthophora retusa, Ceratina callosa, Hoplitis adunca, Megachile apicalis, Megachile centuncularis, Megachile concinna, Megachile parietina, Megachile rotundata, Megachile sicula, Osmia brevicornis, Osmia coerulescens, Osmia cornigera, Osmia cornuta, Osmia emarginata, Osmia fulviventris, Osmia latreillei, Osmia rufa, Osmia nigrifrons, Osmia submicans, Osmia tricornis, Stelis nasuta*

Monodontomerus anthidiorum (Lucas): *Rhodanthidium sticticum*

Monodontomerus argentinus Brèthes: *Eufriesea nigrescens, Megachile* sp.

Monodontomerus bakeri Gahan: *Megachile pugnata, Megachile relativa, Megachile rotundata, Osmia coloradensis, Osmia texana*

Monodontomerus brevicrus Grissell: *Osmia ribifloris*

Monodontomerus clementi Grissell: *Dianthidium heterulkei, Megachile rotundata*

Monodontomerus dianthidii Gahan: *Dianthidium* sp.

Monodontomerus laticornis Grissell and Zerova: *Anthidium florentinum, Anthidium septemspinosum, Apis mellifera, Megachile centuncularis, Megachile rotundata*

Monodontomerus mandibularis Gahan: *Anthophora abrupta, Anthophora bomboides bomboides, Melitoma taurea, Osmia cordata*

Monodontomerus mexicanus Gahan: *Ancyloscelis apiformis, Anthophora marginata, Megachile peruviana*

Monodontomerus montivagus Ashmead: *Anthidium collectum, Anthidium emarginatum, Anthidium ?mormonum, Anthophora abrupta, Anthophora bomboides bomboides, Anthophora bomboides neomexicana, Anthophora linsleyi, ?Anthophora occidentalis, ?Anthophora vallorum, Ashmeadiella californica, Bombus morrisoni, Dianthidium curvatum sayi, Dianthidium pudicum consimile, Dianthidium pudicum, Hoplitis anthocopoides* (nest), *Megachile centuncularis, Megachile relativa, Megachile rotundata, ?Melissodes* sp., *Osmia cordata, Osmia kincaidii, Osmia latisulcata, Osmia lignaria, Osmia ribifloris, Osmia sanrafaelae, Osmia texana, Stelis depressa, Xylocopa tabaniformis orpifex*

Monodontomerus obscurus Westwood: *Anthophora plumipes, Hoplitis adunca, Megachile argentata, Megachile centuncularis, Megachile cephalotes, Megachile flavipes, Megachile lanata, Megachile parietina, Megachile rotundata, Megachile willughbiella, Osmia cordata, Osmia cornifrons, Osmia latreillei, Osmia lignaria, Osmia ribfloris, Osmia rufa rufa, Osmia rufa cornigera, Osmia sanrafaelae, Xylocopa fenestrata*

Monodontomerus osmiae Kamijo: *Osmia cornifrons, Osmia excavata, Osmia taurus*

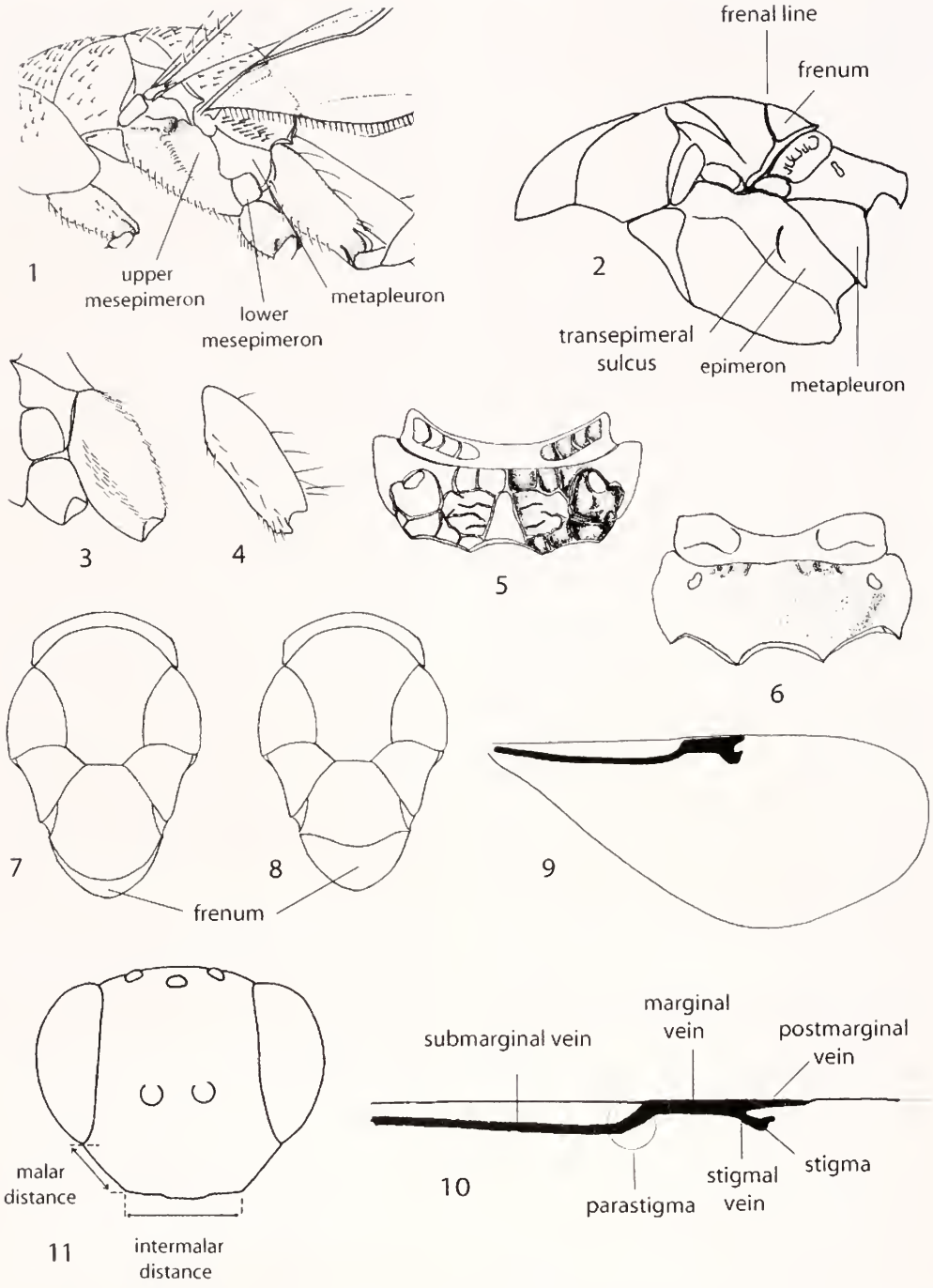
Monodontomerus parkeri Grissell: *Anthophora occidentalis*

Monodontomerus rugulosus Thomson: *Megachile rotundata*

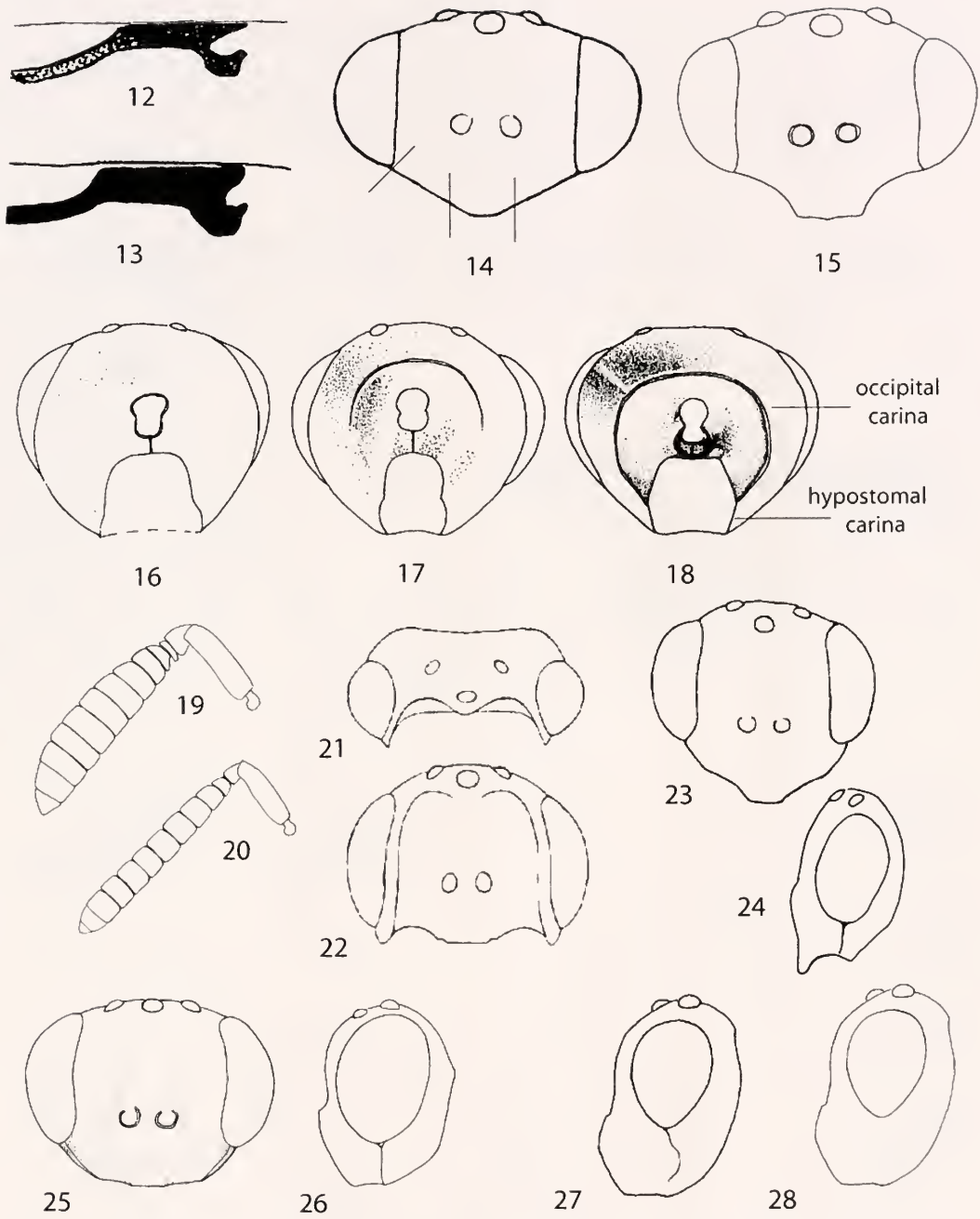
Monodontomerus tepedinoi Grissell: *Osmia lignaria*

Monodontomerus thorpi Grissell: *Anthidium maculatum*

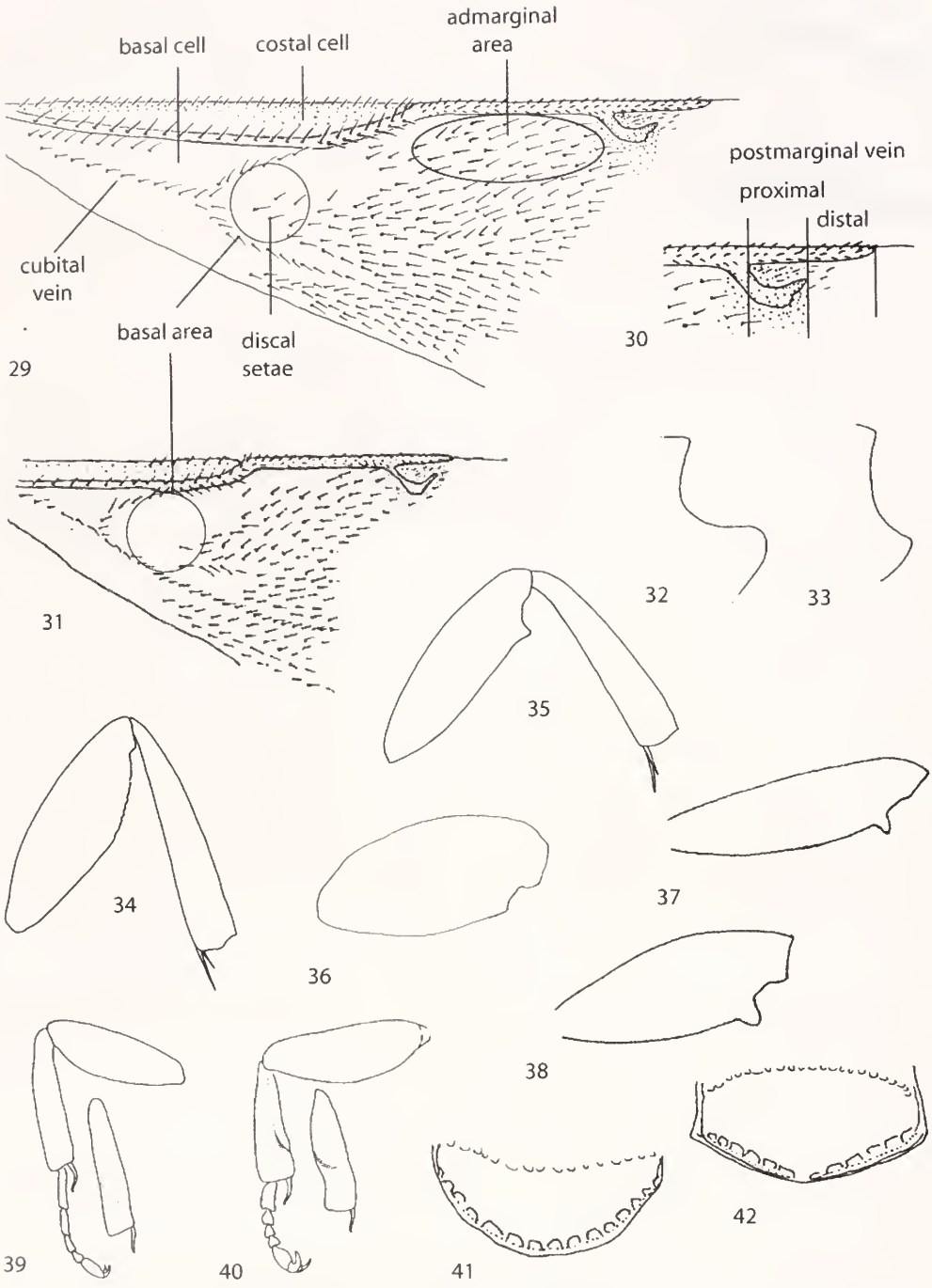
Monodontomerus torchioi Grissell: *Osmia lignaria, Osmia sanrafaelae*



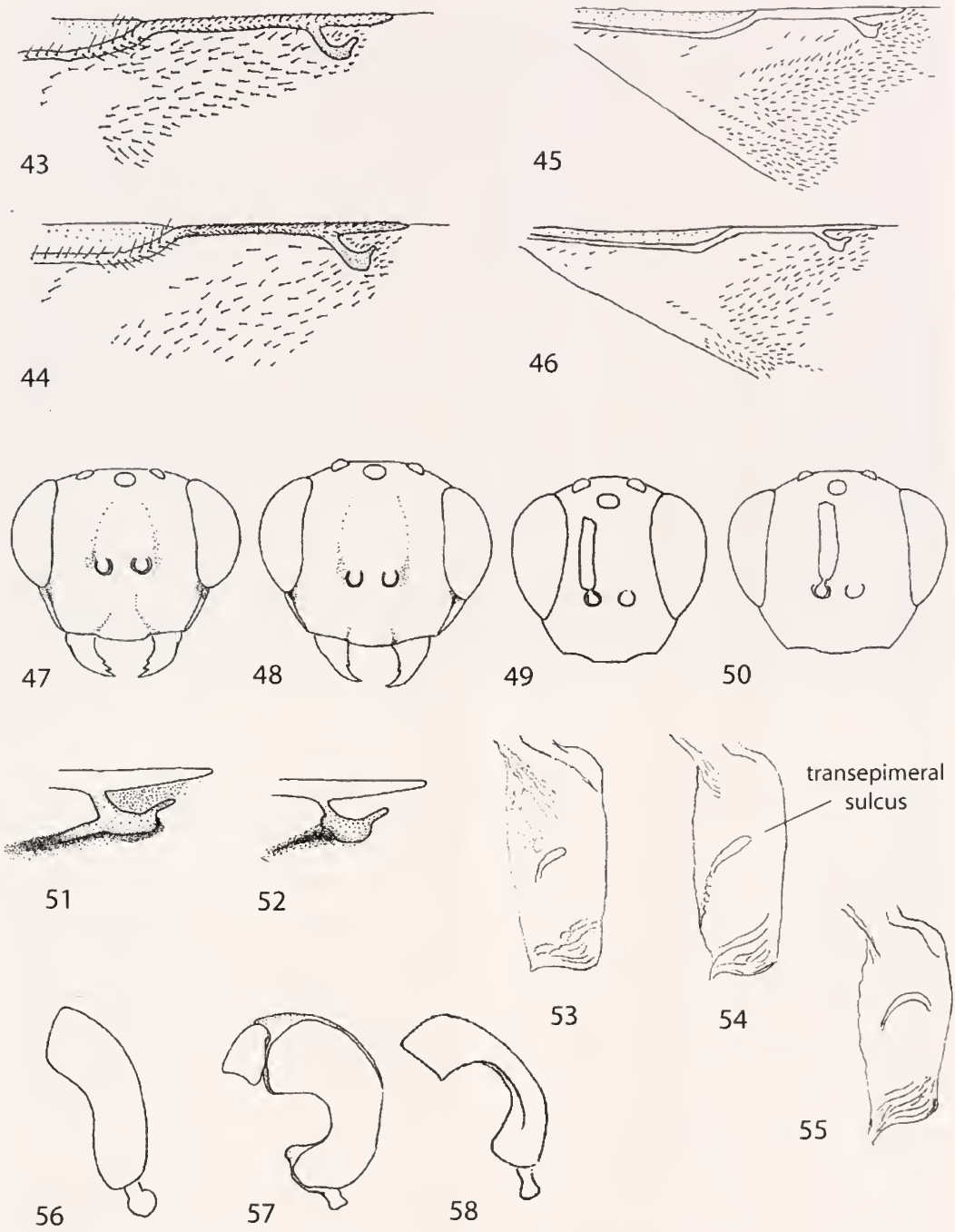
Figs. 1–11. Torymidae. 1–2, Mesosoma, side (arrow indicates anterior margin of metapleuron). 3–4, Metacoxa, side. 5–6, Propodeum, dorsal. 7–8, Mesosoma, dorsal (arrow indicates frenum). 9, Fore wing, dorsal (*Echthrodape africana*). 10, Fore wing, dorsal, showing venation terminology. 11, Head, anterior, showing measurements.



Figs. 12–28. Torymidae. 12–13, Fore wing venation, dorsal. 14–15, Head, anterior, lines indicate malar and intermalar distances. 12, 14 *Echthrodape papuana*. 13, 15 *Echthrodape africana*. 16–18, Head, posterior (showing carinae). 16, *Microdontomerus*. 17, *Pseudotorymus*. 18, *Monodontomerus*. 19–20, Antenna, side. 19, *Monodontomerus thorpi*. 20, *Monodontomerus* spp. 21–28, Head. 21–22, *Monodontomerus osmiae* (from Kamijo 1963). 23–24, *Monodontomerus anthidiorum*. 25–26, *Monodontomerus mexicanus*. 27–28, *Monodontomerus bakeri*.



Figs. 29–42. Torymidae, *Monodontomerus* spp. (except 34, *Pseudotorymus*). 29–31, Fore wing. 29, *M. aeneus*. 30, *M.* sp. 31, *M. clementi*. 32–33, Metasomal tergum 6. 32, *M. argentinus*. 33, *M. rugulosus*. 34–35, Hind femur and tibia, side. 34, *P.* sp. 35, *M. aeneus*. 36–38, Hind femur. 36, *M. thorpi*. 37, *M. argentinus*. 38, *M. rugulosus*. 39–40, Fore leg (left side view, right ventral view). 39, *M. aeneus*. 40, *M. brevicrus*. 41–42, Frenum (apex of scutellum). 41, *M. acrostigmus*. 42, *M. aeneus*.



Figs. 43–58. Torymidae, *Monodontomerus* (*Mo.*) and *Microdontomerus* (*Mi.*). 43–46, Fore wing, part. 43, *Mo. mandibularis*. 44, *Mo. parkeri*. 45, *Mi. parkeri*. 46, *Mi. enigma*. 47–50, Heads. 47, *Mo. montivagus*. 48, *Mo. mandibularis*. 49, *Mi. anthidii*. 50, *Mi. apianus*. 51–52, *M. acrostigmus* (variation in stigma). 53–55, Mesopleuron. 53, *Mo. clementi*. 54, *Mo. parkeri*. 55, *Mo. montivagus*. 56–58, Scape, male. 56, *Mo. montivagus*. 57, *Mo. mandibularis*. 58, *Mo. tepedinoi*.

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Multivoltinism and Usage of Multiple Nest Substrates in a West Texas Sand Dune Population of *Pseudomasaris phaceliae* Rohwer (Hymenoptera: Vespidae: Masarinae)

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Abstract.—A west Texas population of *Pseudomasaris phaceliae* was found to be multivoltine and active from April to September. Unlike previous reports of nests constructed only on stones, nests were commonly constructed on the stems and infructescences of its host plant, *Phacelia integrifolia*. Emergence data indicated the primary sex ratio is strongly female biased (53:14). Nest parasitism was rare, but predation was common. Data on nest architecture, nest construction, and foraging behavior are presented.

Pseudomasaris is the only North American genus of the Masarinae, a relatively small (300+ spp.) but widespread clade of pollen and nectar provisioning vespid wasps (Carpenter 1982, 2001, Gess 1996). Torchio (1970) reported in considerable detail on the biology of *Pseudomasaris edwardsii* (Cresson) but little is known of the biology of the remaining 14 species. Brief reports on nest structure and/or nest sites have been published for eight of these species, including *Pseudomasaris phaceliae* Rohwer, but only floral records are available for four other species, and nothing at all has been published on the biology of the remaining two.

During a brief visit to Monahans Sandhills State Park in June 2005, we encountered a large population of *Pseudomasaris phaceliae* visiting flowers of *Phacelia integrifolia* Torr. (Boraginaceae). *Pseudomasaris phaceliae* is an infrequently collected but sometimes locally abundant species of the arid American Southwest (Arizona, New Mexico, west Texas, and adjacent Mexico) (Richards 1966, and pers. obs.). Although previous reports had indicated that *P. phaceliae*, like most other *Pseudomasaris* species, constructs its nests on stones (Parker 1967, Torchio 1970), we found that at Monahans, *P. phaceliae* was commonly attaching its nests to plant stems, and only rarely to stones. In addition, *P. phaceliae*, like most other temperate masarine species, had previously been assumed to be univoltine (Parker 1967, Gess 1996), but wasps emerged in early July from a nest collected during June suggesting multivoltinism. This prompted a series of visits to this site to gather additional information on the nests and behavior. Follow-up trips were made in July, August, and September 2005 and April, May, June, and August 2006.

Habitat.—Monahans Sandhills State Park (32.128° N, 103.953° W) is located in Ward County, Texas on the southern edge of a large dune field of quartz-rich Quaternary sands that stretch northward into southeastern New Mexico (Machenberg 1984, Muhs 2001). While much of the dune field is partially stabilized by shin oak (*Quercus havardii* Rydb.) and other perennials, large moving dunes are common in

Figs. 1–2. 1. *Pseudomasaris phaceliae* nest (indicated by arrow) on *Phacelia integrifolia* stem. 2. Incomplete *P. phaceliae* nest with one completed cell and one cell under construction.

the Park. Soils in the sandhills consist almost exclusively of loose sands. Occasionally, winds expose the underlying caliche layer, but generally there are no rocks or stones in the dunes beyond those brought in for the caliche service roads. Like most of Texas, summers are warm with July maximum temperatures averaging 35° C. Rainfall is low, averaging 33.6 cm per year, with 75% of precipitation occurring during a six-month May to October summer/fall period. Despite the relative aridity, the water table is quite shallow in the sand hills due to an underlying impermeable caliche layer. Water-loving plants like *Salix nigra* Marshall (Salicaceae) and *Baccharis salicina* Torrey & A. Gray (Asteraceae) are found in some of the deeper depressions among the dunes where temporary ponds may form following unusually heavy rains (Machenberg 1984).

Nests.—Although a few nests were found on miscellaneous plant stems (such as a sapling of *Prosopis glandulosa* Torr. (Fabaceae) or stems of the erect herb *Mentzelia strictissima* (Wooton & Standl.) J. Darl. (Loasaceae), the vast majority of the nests we found were on stems or infructescences of larger (over 40 cm high) individuals of *Phacelia integrifolia* (Fig. 1.). Nests were located at heights of 20.3–71.1 cm above the ground (n=50, mean = 41.0 ± 9.9 cm). Typically there was only one nest per plant although a few plants had two, and one *Phacelia* plant had four nests, two older nests from which emergence was complete, and two newer nests under construction.

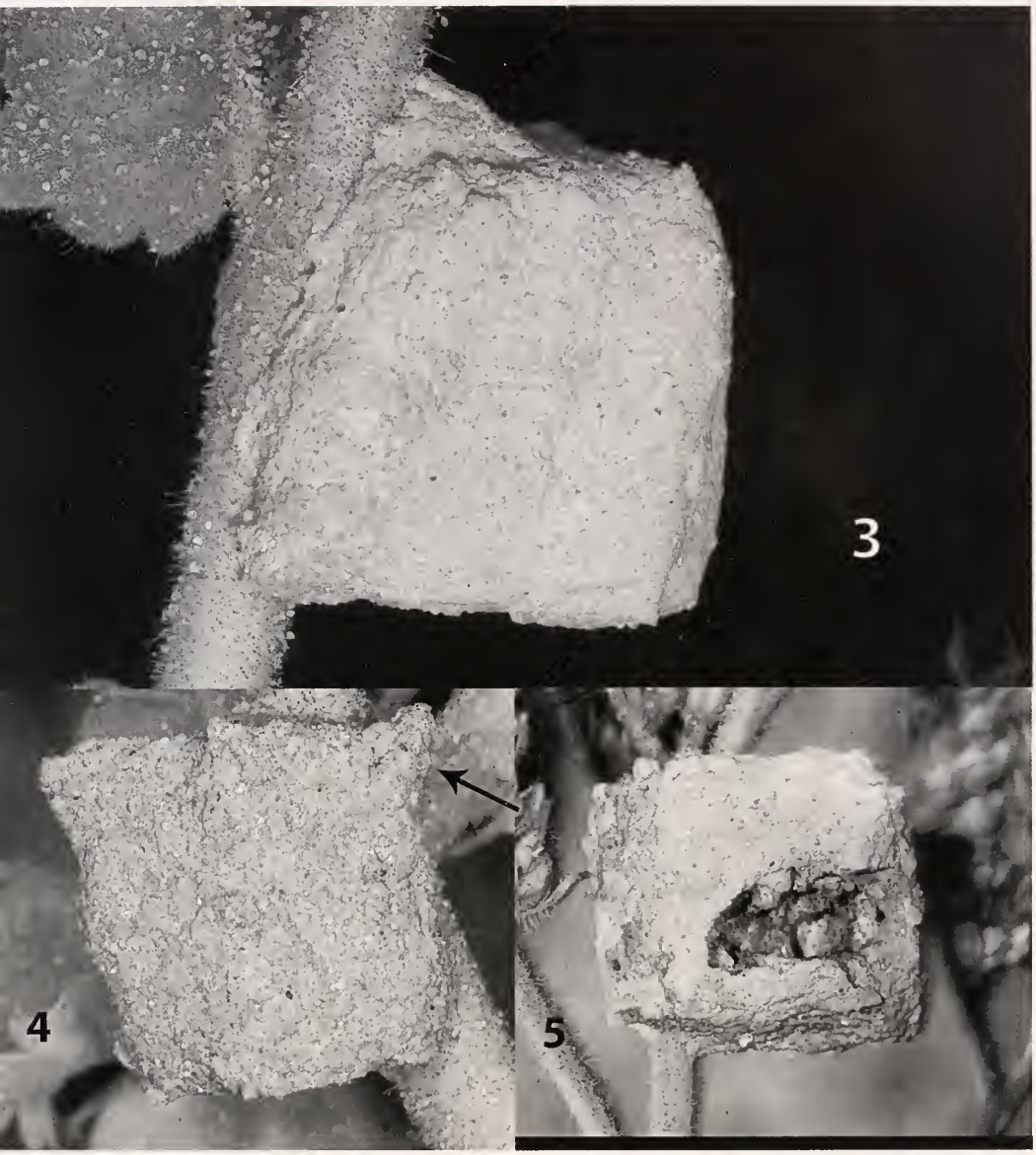
Like those of other *Pseudomasaris* species, nests consisted of one or more cylindrical cells attached lengthways one to another (Torchio 1970). Cells of nests on plants were always positioned with the long axis

oriented vertically, regardless of the orientation of the stem or infructescence (Fig. 2). Nests on plants averaged 5.4 ± 3.8 cells per nest, (1–14, n = 53), a value that probably underestimates the true number of cells per nest since some of the nests may not have been complete when censused. Nests on stems were initiated by laying down a strip of the sand-soil mix along a stem or infructescence. The female then constructed the hemispherical inner end of the cell at the upper end of the strip, and completed the cell wall by adding irregular strips or scale-like patches of the moist sand-soil mix. Upon returning with a sand-soil load, the female inserted her head in the nest and curled her metasoma so its tip was opposite her head. The moist sand-soil mix was added to the cell wall by simultaneously working the mix from within with her mandibles and tapping it from the outside with the flattened, hirsute surface of metasomal sternite 6. Time on the nest depositing cemented sand was typically brief (0.6–2.9 min).

The first cell is a true cylinder as the walls are complete, the plant substrate not being used as part of the cell wall (Fig. 2). Additional cells are attached to the walls of the initial cell so the nest grows in an asymmetrical manner away from the stem rather than around it (Fig. 3). Cell walls are rather thin, only 0.4–0.5 mm thick, but quite strong. Nests within 100 meters of the caliche road were usually constructed with a mix of relatively coarse sand particles (0.1–0.4 mm in diameter), and much finer (0.02–0.04 mm) particles, presumably caliche dust. Nests further from the road are constructed of sand alone. The particles are bound together with regurgitated nectar, and perhaps, glandular products. As there was no free water in the dunes, nectar (or perhaps honey-dew) was the only likely source for the bulk of the liquid used to moisten the sand-soil mix. Nest fragments placed in water softened but were still intact after being immersed for 48 hours, suggesting substances beyond just sugar may be holding the walls together. These moistened nests quickly sprouted fungal hyphae, the fungi presumably growing on the nectar sugars. In contrast, the true mud nest walls and partitions of nests constructed by *Trypargilum politum* (Say) or *Osmia lignaria* (Say) dissolve almost instantly when placed in water (pers. obs.).

Individual cells were 15.2 ± 1.2 mm (12.8–17.6, n = 19) mm long with an average diameter of 4.2 ± 0.2 mm (3.8–4.5, n = 28). The distal end of the cell was hemispherical while the cell opening was simple and truncate. After provisioning, each cell was closed with a cemented sand plug 0.5–0.8 mm thick medially and 1.0–1.3 mm thick at the sides. Additional sand and fine particles were added to the nest exterior as construction proceeded, filling the spaces between the cells (Fig. 9). In one unfinished nest in which the second cell was only half finished, soil had been added along the juncture of the two cells, strengthening their connection, although additional soil had not been added elsewhere to the outer surface of the first cell. Upon completion, the nest has flattened, relatively smooth walls concealing the outlines of individual cells. We found no indication of empty spaces between the cells. Completed nests on stems usually lacked obvious ornamentation but a few (4 of 50) had conical projections on the margins of the nest (Fig. 4).

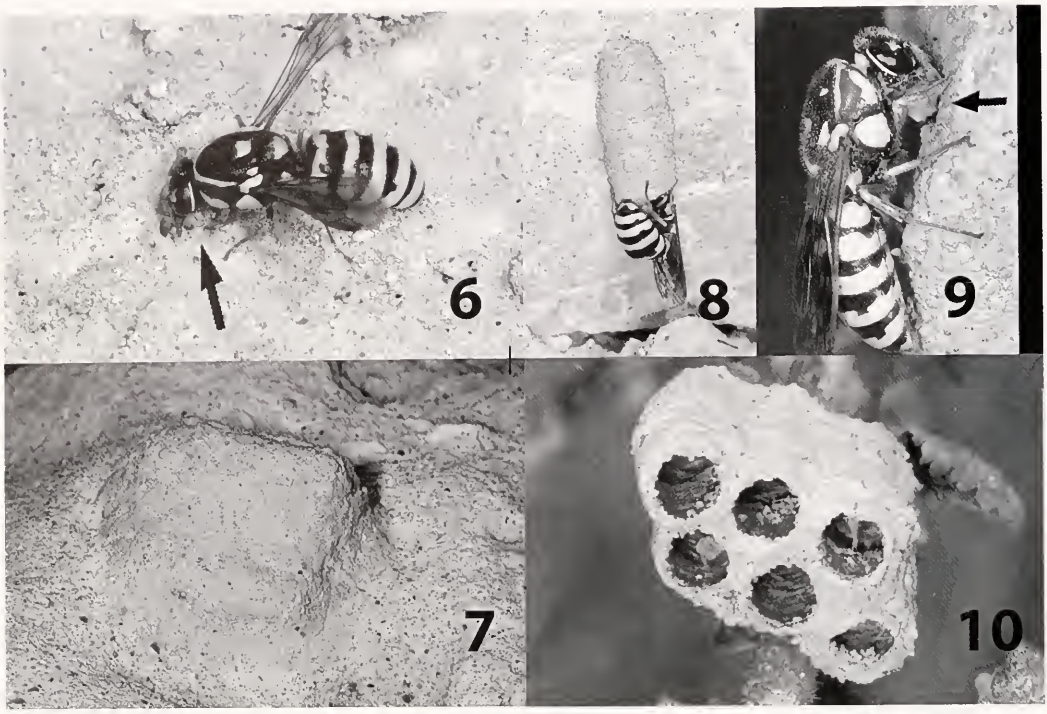
Females were commonly observed collecting fine soil particles along the caliche road (Fig. 6) and, less frequently, in the dunes. Females would hover 10–15 cm above the soil surface and repeatedly drop to collect sand or soil. We did not obtain a complete picture of soil collection but it was clear that during most bouts on the soil surface, the wasps did not add nectar to the soil surface prior to collection. Rather, they used their mandibles and foretarsi to add soil or sand to a moist soil bolus held behind the mandibles by their modified labial palpi. Regurgitated nectar



Figs. 3–5. 3. Completed *Pseudomasaris phaceliae* nest showing asymmetrical position on *Phacelia integrifolia* stem. 4. Ornamented *P. phaceliae* nest (projection indicated by arrow). 5. *P. phaceliae* nest opened laterally, probably by birds.

is apparently added to this bolus while the wasps are hovering. As in *Pseudomasaris edwardsii*, females constructing cells or adding sand to the nest exterior typically made long trips (20–30 min duration) to gather nectar at flowers as well as sand, interspersed between series of 3–4 relatively short (0.9–3.1 min) trips. The latter trips were presumably for sand only since they were too brief to allow for both sand and nectar collection.

While the majority of nests were constructed on plant stems, some nests were constructed on small stones brought in for a caliche service road through the dunes. These were structurally similar to the nests



Figs. 6–10. 6. *Pseudomasaris phaceliae* female collecting sand (sand bolus indicated by arrow). 7. Completed *P. phaceliae* nest on stone. 8. Female extending walls of new *P. phaceliae* nest. 9. Female adding sand (indicated by arrow) to exterior of *P. phaceliae* nest. 10. Emergence holes from six- celled *P. phaceliae* nest.

constructed on stems, but had fewer cells, never more than three, averaging only 1.3 ± 0.5 cells (1–3, n = 28). While all the stem nests were constructed during the year in which they were discovered, many of the rock nests were worn and/or damaged and may have been constructed in prior years. Unlike the situation in stem nests, the first cells constructed on stones were usually not true cylinders as the stone was used as part of the cell wall. The first cells constructed typically were attached to the stone along their entire length (Fig. 8), although in a few cases, only the basal half of the cell was attached to the substrate, with the outermost portion arching away. Completed nests on stones often appeared to be triangular in cross-section, due to the smoothing of the sides and the addition of soil, which greatly widened the base of the nest (Fig. 7). Nests on rocks occurred both on the sides and upper surfaces without any consistent orientation. Completed nests on stones were quite cryptic as the outer nest covering matched the color of the pale stone on which they were constructed. Nests on *Phacelia* plants were more conspicuous since the pale nests contrasted with the green stems or young infructescences, but the nests were still somewhat cryptic since the infructescences, leaves and/or leaf tips all commonly turn brown with age.

Nests are provisioned with a dense mass of regurgitated pollen-nectar pellets. The pellets had short projections and were oriented so the projections, rather than the main mass of the pellets, contacted the cell walls. Pellets averaged 0.6–0.7 mm across with projections from 0.2 to 0.6 mm long. Unlike the provisions of *Pseudomasaris edwardsii*, the innermost face of the provision mass of *P. phaceliae* was not smoothed so the individual pellets were easily distinguished. The outer face of the provision mass (the surface facing

the cell closure) was smooth and convex. We found several cells being provisioned, and others with feeding larvae but recovered only a single cell with a completed, intact, provision mass. This mass was 15.2 mm long, occupying nearly all the cell, leaving a small open space of 0.8 mm between the mass and the roof of the hemispherical inner end, and 1.6 mm between the mass and the cell closure.

Host Plant and Foraging.—Pseudomasaris phaceliae is believed to restrict its foraging to flowers of *Phacelia* spp. (Torchio 1970). At Monahans dunes, individuals of *P. phaceliae* foraged only at flowers of *Phacelia integrifolia*, the only *Phacelia* species flowering. *Phacelia integrifolia* is a widespread annual of the American Southwest, occurring on a variety of rocky or sandy substrates, particularly gypsum or limestone (Correll and Johnston 1970). The plants bear scorpioid cymes of small, pale purple flowers. In west Texas, flowering occurs primarily from March through May (Correll and Johnston 1970), although herbarium records from the Plant Resources Center of the University of Texas, Austin, Texas, show flowering as late as the end of July in the Monahans Sandhills area, and a non-technical guide indicates flowering through September (Ajilvsgi 2003). *Phacelia integrifolia* was common and in flower during our first 2005 visit to Monahans dunes on 16 April, although cold, wet weather prohibited any observations of floral visitors. When we revisited Monahans Dunes on 18 June 2005, we found *P. integrifolia* flowering was still widespread although most abundant in certain depressions between the dunes. When the site was revisited a month later in July, most *P. integrifolia* plants on the dunes were brown and dead, and flowering was restricted to the large plants occurring in the depressions between the dunes. Unlike the typical, erect plants on the dunes and most other habitats (Fig. 1), these plants were sprawling and multibranched, almost shrub-like in aspect, with greatly enlarged stems. These depression plants were still strongly flowering when the site was revisited in August. On the final 2005 visit on 16–18 September low levels of flowering were still occurring among the large depression plants although most plants were dead, and flowering was limited to a few inflorescences. On 21 April 2006, *P. integrifolia* was flowering and locally abundant on the dunes, but surprisingly, was absent in the depressions where the large, long-flowering individuals were found in 2005. Flowering continued, with a gradual decline in overall abundance through May and June 2006. By August 2006, only secondary inflorescences of the few surviving individuals were still flowering.

Individual flowers of *Phacelia integrifolia* begin opening around 0830 CDT (approx. 2 hrs after sunrise), and flowers continue opening through the day. Individual flowers last approximately two days. Anthers dehisce fully shortly after flower opening, and are usually stripped of pollen within two hours of opening. Some larger bees, such as species of *Habropoda*, *Osmia*, or *Martinapis* began foraging on *P. integrifolia* at or before 0800 early in the season, but *Pseudomasaris phaceliae* was always a late starter. Females were rarely observed before 0830 CDT and they were generally not active until after 0930 CDT with air temperatures above 30 C. Foraging continued until sundown, although females were sometimes observed resting on stems or branches during periods of peak heat in late afternoon (air temperatures above 39 C).

Foraging rates recorded on 13 July 2005 were quite rapid, perhaps a reflection of the high temperatures (33–35 C) and resource depletion due to the high number of wasps and bees concentrated on the relatively few *Phacelia* plants still flowering. Wasps visited an average of 24.5 ± 5.3 (16.4–31.2, n = 20) *Phacelia* flowers per minute. Nectar visits were quite quick, averaging only 0.8 ± 0.3 (0.3–2.0, n = 40)

Figs. 11–12. 11. *Pseudomasaris phaceliae* female collecting pollen of *Phacelia integrifolia*. 12. *P. phaceliae* female nectaring at flower of *P. integrifolia*.

seconds per flower while pollen-collecting visits were longer at 4.1 ± 3.0 (1.1–11.2, n = 20) seconds. During a foraging bout, the proportion of flowers worked for pollen was low, averaging only 13.7 ± 14.6% (0–41.7, n = 20). This is presumably a reflection both of the low availability of fresh flowers with available pollen, and the fact that some foragers were constructing their nests and not foraging for pollen at the time. If we exclude foraging series where no flowers were visited for pollen, the proportion of flowers visited for pollen rises only slightly to 19.6 ± 13.7% (3.4–41.7, n = 14).

A nectar foraging bout involved landing on medial portions of the exserted staminal filaments and rapidly inserting the remarkably extensible proboscis (~ 4.5 mm long when fully extended) to reach the nectary at the base of corolla tube (Fig. 12). The initial approach to a flower presumably involved some assessment of pollen availability, since foraging behavior changed when a pollen forager encountered a flower with obvious available pollen. A pollen forager would grasp the staminal filament near the anther with her hind and mid-tarsi while hovering (Fig. 11). She would then grasp an anther with her mandibles and extract pollen by scraping pollen to her mouthparts with the tarsal brushes of her forelegs. Depending on pollen availability, a wasp might work several anthers on a flower before moving down the filaments to insert her mouthparts to gather nectar.

A female observed on 17 June 2006 took 8.40 hrs and 15 foraging trips to provision a cell. Pollen foraging appeared to commence immediately after oviposition. Because of poor light conditions, we were not able to determine if the female deposited an initial pollen and nectar load immediately after ovipositing as has been reported for *Pseudomasaris edwardsii* (Torchio 1970). Pollen trips averaged 31.53±7.10 min (19.32–41.72, n=13) and deposition time in the nest between trips averaged 2.06±0.48 min (1.50–3.52, n=14). As noted for *P. edwardsii* (Torchio 1970), the female rotated within the cell during the later phases of pollen deposition as she deposited pollen pellets.

Development and Voltinism.—Only fragmentary data were obtained on development. The only intact egg recovered was smooth, slightly asymmetrical, and 3.7 mm long with a medial width of 1.0 mm. The posterior end of the egg was attached

Table 1. Collection dates for nests of *Pseudomasaris phaceliae* from Monahans Sandhills with emergence dates and sex ratio of the wasps.

Nest	Collection date	Emergence date	Males	Females
H-1	16-vi-2005	by 12-vii-2005	1	14
N-1	18-vii-2005	19-vii-2005	0	2
N-2	18-vii-2005	23-vii-2005	0	1
N-3	18-vii-2005	3-iv-2006	0	1
N-4	15-viii-2005	28-viii-2005	1	3
N-5	15-viii-2005	1-ix-2005	0	1
N-6	18-vii-2005	19-iv-2006	0	2
05-06	18-vii-2005	approx. 3-iv-2006	0	1
05-07	18-vii-2005	approx. 3-iv-2006	1	1
05-02	18-vii-2005	18-iv-2006	2	0
06-01	23-iv-2006	26 to 29 iv-2006	1	5
06-02	19-v-2006	1 to 7 vi-2006	1	8
06-03	18-vi-2006	27-vi to 11-vii-2006	1	7
06-04	18-vi-2006	1 to7 vii-2006	4	3
06-05	18-vi-2006	5 to11 vii-2006	1	3
06-06	18-vi-2006	12-vii-2006	1	1
Total			14	53

perpendicularly to the inner surface of the cell wall, just below the hemispherical, inner end of the cell. The ventral surface of the egg, which paralleled the flat inner surface of the provision mass, was somewhat flattened, but the dorsal surface of the egg arched slightly into the curved space of the hemispherical inner cell cap. In two instances where late instar larval feeding was noted, the larva fed along the side of the provision, eating its way down the provision mass toward its distal end. Sometime after completing feeding, the larva spun a thin, translucent cocoon that adhered tightly to the cell wall. Defecation occurred after the completion of the cocoon. Feces were typically deposited as an irregular ring of smooth, flattened, semispherical pellets (0.8–1.0 mm wide, and 0.5–0.6 mm tall), around the inner end of the cell, although some of these are sometimes pressed into a flattened cake with unrecognizable individual pellets. Nest dissections indicated wasps overwinter as prepupae. Adults emerge by chewing through the nest plug (Fig. 10).

The total number of generations per year of *Pseudomasaris phaceliae* at Monahans is unknown but at a minimum it is two and perhaps as many as four. *Pseudomasaris phaceliae* was active at Monahans for at least 93 days (18 June to 18 September) in 2005 and 116 days (26 April to 19 August) in 2006. Judging from the extensive wing wear of females collected in June of 2005, the phenology of *Phacelia integrifolia*, and the emergence times of *P. phaceliae* in the lab (Table 1.), flight at Monahans during 2005 probably began in early April suggesting a flight period in excess of 156 days in 2005.

Emergence patterns of wasps from nests collected in 2005 and 2006 are indicated in Table 1. All nests collected before July had their inhabitants emerge that same year, but for nests collected in July or later, some emerged the same year but others went into larval diapause and emerged the following April. The instances of late 2005 (July to September) emergence were from nests taken from infructescenses on relatively fresh green plants, and it is clear that they had been provisioned in 2005. *Phacelia integrifolia* stems usually break down completely over the winter and the glandular epidermis, to which the nests are frequently attached, falls away soon after the plant dies. It is probable that over-wintering

nests fall from the disintegrating plants and spend the winter in the sand.

Mating and Sex Ratio.—Males of *Pseudomasaris phaceliae* were observed to forage for nectar at plants of *Phacelia integrifolia* and patrol *P. integrifolia* inflorescences, but mating was not observed. Newly emerged males confined with newly emerged female nest mates attempted to mount their sisters, although it was not determined if mating was successful. Females were much more common than males at flowers at all times during our visits, and the sex ratio of wasps emerging from nests was heavily female biased 3.8:1 (53 females/14 males, Table 1). In all cases where emergence order was determined, males emerged from the first provisioned cell(s) of a nest.

Nest Associates and Predators.—Nest parasitization was uncommon. One female *Chrysurissa densa* (Cresson) (Chrysididae) emerged on 18 July 2005 from a *Pseudomasaris phaceliae* nest and a second female emerged from a different nest on 13 September 2005. *Chrysurissa densa* apparently is a specialist on *Pseudomasaris*, since besides *P. phaceliae*, its only known hosts are four other *Pseudomasaris* species. In addition, its range mirrors that of *Pseudomasaris* (Bohart and Kimsey 1982). The only other nest parasites where 10 females and 2 males of an unidentified *Monodontomerus* sp. (Torymidae) which emerged from a cell of another nest of *P. phaceliae*. As parasite emergence occurred only two days after collection of the nest, it was clearly the result of field, rather than laboratory, infestation.

Indications of nest predation were occasionally encountered. Several nests observed in 2005 and 3 of 21 nests measured in June 2006 had all their cells opened laterally (Fig. 5). The cells in these nests contained empty cocoons but had intact cell caps. Birds are the most likely predators although we cannot rule out small mammals. A small, unidentified woodpecker was seen perching and searching on *Phacelia* stems, but actual nest predation was not confirmed. Additionally, two newly provisioned cells were encountered with small lateral slits, possibly the results of bird probes. One of these probed cells contained a larva and partially consumed pollen mass while the other was being raided and emptied by ants.

We found no indication of empty (closed but unprovisioned) cells in *Pseudomasaris phaceliae* nests at Monahans. Empty cells have been invoked as an anti-parasite defense strategy for *Pseudomasaris vespoides* (Cresson), in which roughly 30% of the nest cells are empty (Tepedino et al. 1979).

DISCUSSION

Our observations of *Pseudomasaris phaceliae* at Monahans suggest this species has a broader behavioral range than previously observed in *Pseudomasaris*. The most obvious differences from previous reports are the incidence of multivoltinism and use of plant stems for nest placement. Multivoltinism has not previously been reported in *Pseudomasaris* and appears to be rare in the Masarinae, at least among temperate zone species (Gess 1996). Presumably, this is true because these wasps are typically oligolectic (or at least have a narrow range for floral hosts) and the flowering periods of their floral hosts usually are quite temporally restricted. Multivoltinism is possible at Monahans because of the unusual extended flowering of its floral host in this distinctive habitat, allowing a flight season that can extend from April into September in favorable years. However, it is possible that multivoltinism occurs in other non-dune populations of *P. phaceliae* associated with *P. integrifolia*. We have collected *P. phaceliae* on this species at other west Texas sites in June. Wing wear indicated these wasps were relatively newly emerged even though the few flowering *P. integrifolia* plants at these sites were in very poor condition and most plants in the populations were dead or fruiting.

As we encountered neither flowering *Phacelia* nor *Pseudomasaris phaceliae* during

July, August, or September visits to Monahans prior to 2005, multivoltinism may be a facultative phenomenon for *P. phaceliae*. The wasps could use environmental cues such as temperature and humidity, which may predict extended *Phacelia* bloom, to "determine" whether to pupate and emerge immediately or proceed to diapause. Increasing humidity, a predictor of flowering in desert plants, has experimentally been shown to be an important cue in breaking diapause in *Macrotera portalis* Timberlake (Andrenidae), a desert bee with extended diapause (Danforth 1999), while temperature (above or below 29 C) determines whether *Nomia melanderi* Cockerell (Halictidae) pupates and emerges immediately or proceeds to diapause (Stephen 1965). Even in years with extended *Phacelia* flowering, flowering declines greatly late in the year. The observation that some larvae in late provisioned nests (July or later) pupate and emerge immediately while others diapause until the following spring suggest a bet-hedging strategy predicated on the decreasing chances of encountering adequate floral resources late in the year.

Published reports have indicated that surfaces of rocks are the preferred nest substrates utilized by six *Pseudomasaris* species (Hicks 1929, Hungerford 1937, Parker 1967). In Torchio's 1970 glasshouse study, *Pseudomasaris edwardsii* females constructed nests on a variety of substrates, but not plant stems. However, the use of bamboo stakes as a nest substrate in Torchio's study suggests they may occasionally use twigs or plant stems under natural conditions. The only report on *Pseudomasaris texana* (Cresson) indicates it constructs its nests on twigs (Bequaert 1940). *Pseudomasaris vespoides* has repeatedly been reported constructing its nests on twigs or plant stems (Cockerell 1913, Davidson 1913, Hicks 1929, Bequaert 1940, Torchio 1970), although it also is known to use rocks (Hicks 1927). *Pseudomasaris marginalis* (Cresson) was found to nest in beetle borings in logs at a high altitude site in Colorado (Dorr and Neff 1982) although this report has been questioned (Gess 1996). In the only previous report on the biology of *P. phaceliae*, rock surfaces were the only reported nest substrate (Parker 1967).

Since rocks are rarely encountered in the Monahans Sandhills, it is not surprising that most of the *Pseudomasaris phaceliae* nests we encountered were attached to plants. The relative advantages of rock surfaces and plant stems as nest substrates are unclear. Rock surfaces are obviously more permanent and stable than herbaceous plant stems, but the importance of this difference is not clear for wasps like these that do not reuse their nests. The issue of difference of substrate permanence could easily be erased by using the stems of perennials, although *P. phaceliae* does not seem to regularly do this at Monahans. If heat stress is a problem, a strong possibility in a habitat like Monahans Sandhills where soil surface temperatures regularly exceed 40° during the late spring and summer, constructing nests well above the soil surface on plant stems might be advantageous relative to building nests on low, exposed rock surfaces.

The nest biology of most *Pseudomasaris* species is poorly known, often based on only a single population, and, in some cases, a single nest. When the biologies of more populations of more species of *Pseudomasaris* are known, it will be interesting to see if other *Pseudomasaris* species are similarly flexible in their patterns of voltinism and/or nest substrate usage.

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Mydrosoma micheneri Packer, new species, a New Diphaglossine Bee from Brazil (Hymenoptera: Colletidae)

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Abstract.—***Mydrosoma micheneri* Packer, new species**, is described and illustrated. The sole known specimen, a female, is from the Mato Grosso of Brasil and was collected almost 40 years ago. It is distinctive in having a longer head and malar space than other members of its tribe.

The purpose of this paper is to describe a somewhat unusual species in the genus *Mydrosoma*. It differs from other species by the comparatively elongate malar space and clypeus. The genus *Mydrosoma* is one of three genera in the tribe Dissoglottini, the others being *Mydrosomella*, with two species (Graf and Urban 2001), and the monotypic *Ptiloglossidia* (Michener 2007). *Mydrosoma* occurs from southern Brazil to Mexico and none of its nine species have been collected frequently. The only biological data suggest that these may be late afternoon flying bees, with short activity periods; this could help explain their apparent rarity.

In the description below, standard terminology for bee morphology is employed, following Michener (1986, 2007). Puncture density is indicated by the relative distances between punctures in terms of interspace (i) to puncture diameter (d) ratios (e.g. i = 2d). Flagellomeres are numbered 1–10, and metasomal terga and sterna indicated by T and S, respectively. Hair length is indicated relative to the diameter of the median ocellus – MOD.

Mydrosoma micheneri Packer new species
Figs 1–2

Diagnosis.—The new species has the standard combination of characteristics of the tribe Dissoglottini: pre-episternal groove absent and notaulus weak or absent. It is clearly a member of the genus *Mydrosoma* as indicated by the presence of arolia, second and third submarginal cells subequal in area and basitibial plate incomplete. The new species is readily separated from other *Mydrosoma* by the comparatively elongate head, with clypeus only 1.5 times as wide as long and malar space almost as long as basal depth of mandible (Fig. 1).

Description.—Female. Body length 14 mm, forewing length 9 mm, head width 3.05 mm, intertegular span 2.8 mm.

Colouration: Black with lower face, antenna, legs and metasoma dark brown; following parts orange: anterior surface of flagellum (except F2 red-brown), entire apical flagellomere, tegula, fore tibia and fore tarsus, wing veins; wing membrane pale amber; metasomal terga with metallic reflections; apical impressed areas straw.

Pubescence: Hairs plumose with numerous short branches. Bright fuscous on dorsal and lateral surfaces of mesosoma, pale yellowish on face, ventral surface of mesosoma, legs and metasoma. Outer surface of hind tibia with brown hairs. Prepygidial fimbria dark brown, hairs on disks of T2–T5 blackish. Hairs on face short, 1.5MOD; slightly longer on vertex, genal area and mesoscutum, 2MOD; longer on mesopleuron, scutellum and metanotum ≤3MOD; longest hairs on lateral

Fig. 1. Lateral habitus of *Mydrosoma micheneri*, Packer, n. sp.

surface of propodeum and hind femoral scopa, 4MOD. Hind tibia with shorter hairs ≤2MOD except longer on ventral surface <3MOD. T1 with simple erect hairs 2MOD, longer and plumose laterally, 3MOD. Apical bands of appressed hairs on T2–T4 <2MOD. S1 with short erect hairs, 1.5MOD; S2–S5 with posteroventrally directed long subapical hair bands, hairs with numerous branches on anterior of rhachis only, longest on S3, 3.5MOD.

Surface sculpture: Microsculpture weak, surface shiny, except somewhat dull on lower face. Punctures on face below antennae distinct and moderately dense i ~ d; frons with punctures finer and shallower but equally dense; narrow transverse impunctate band between antennal bases; area between lateral ocellus and compound eye and vertex immediately behind ocelli almost impunctate. Mesoscutum with shallow, moderately dense punctures, i ≤ d; scutellum with deeper, more distinct and irregularly spaced punctures, i = 1–3d; metanotum with punctures almost crowded laterally, i > d medially; dorsal area of propodeum impunctate, lateral surface densely punctate above and along ventral margin, i ≤ d, sparsely punctate below; mesopleuron with dense, somewhat effaced punctures, almost crowded dorsally, i < 1.5MOD below; T1 with punctures sparse on disk, i = 2–4d, denser towards submarginal zone i = 1–2d; punctures increasingly dense on more posterior terga, i ≤ d on T5. Apical impressed areas with tiny dense punctures apically.

Structure: Head as wide as long. Labrum flat with weak transverse basal ridge. Mandible three times as long as basal depth, subapical tooth short. Galeal comb with approximately 28 teeth. Clypeus 1.5 times as wide as long, apical rim slightly upturned. Supraclypeal area 1.25 times as

Fig. 2. Frontal view of head of *M. micheneri* Packer n. sp. to show elongate mandible, clypeus and malar area.

long as apical breadth. Interantennal distance 0.75× antennocular distance. Malar space long, ~0.87× as long as basal depth of mandible. Genal length subequal to width of compound eye; longitudinal axis of compound eye just posterior to mid-depth of mandible; almost at right angle to axis of mandible base. Facial fovea indistinct, marked by weak ridge at inner margin of upper paraocular area approximately 1.5MOD in length. Ocellocular distance subequal to interocellar distance and less than twice MOD. Vertex behind lateral ocellus subequal in length to MOD, weakly depressed. F1 equal to combined lengths of F2 and F3; F2–F9 somewhat broader than long, F10 almost twice as long as wide. Notaulus not evident. Scutellum weakly depressed medially. Dorsal surface of propodeum convex, mostly declivous. Basal vein thickened for apical half. First recurrent vein enters second submarginal cell two vein widths from 1r-m. Posterior margin of second submarginal cell 10% longer than that of third submarginal cell. Basitibial plate indicated by posterior carina 2.5MOD in length. Hind basitarsus twice as long as greatest depth, dorsal margin strongly and ventral margin weakly convex. Jugal lobe slightly less than half as long as vannal lobe.

Male.—Unknown.

Etymology.—It is a pleasure to name this species after Charles Michener in recognition of his stellar achievements in melittology.

Material Studied.—Holotype female: BRAZIL: Mato Grosso 12°50′S 51°47′W, 2.iv.1968. O.W. Richards. A second label states: R.S. & R.G.S. Expedition B.M. 1968–260. A third label states "Gallery forest". A fourth, handwritten, label states "Paracolletini, n. gen. N. sp.!" [Though the species is clearly a member of the Diphaglossinae

as indicated by the tiny stigma and strongly bifid glossa.] The specimen belongs to the Natural History Museum (BMNH).

Comments.—This species keys out to *M. inusitatum* (Snelling) in Michener (1986), but can be easily distinguished from that species by the malar area which is longer than in all other species of *Mydrosoma*, but linear (absent) in *M. inusitatum*. It might seem to belong to Friese's *Bicornelia* (sunk within *Mydrosoma* by Michener 1986; see also Snelling 1980), although that species group is defined based upon secondary sexual characteristics of males, which are unknown for *M. micheneri*. It does not key out to either species of "*Bicornelia*" using Michener (1986).

The locality where the species was collected is now largely agricultural, although gallery forest remains along watercourses. There is a substantial area of forest to the west of the type locality however, the Parque Nacional do Xingu. It is possible that this species may persist in this region.

ACKNOWLEDGEMENTS

I am grateful to George Else (BMNH) for the opportunity to borrow the specimen described herein. Jason Gibbs prepared the images in figures 1 and 2, for which I am grateful. Funding for my research is provided by the Natural Science and Engineering Research Council of Canada.

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Phenology and Social Organization of *Halictus* (*Seladonia*) *tripartitus* (Hymenoptera: Halictidae)

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Abstract.—We present data on the social biology of *Halictus* (*Seladonia*) *tripartitus* Cockerell based upon samples from California. This bee is at least partially eusocial and overwintered gynes and first brood workers differed in size by 5.14%. 35.5% of the first brood workers had developed ovaries, 11.2% had ovaries with the equivalent of at least one fully developed oocyte but less than 14% were mated. In July and August, female reproductive options seemed highly variable: approximately 55% were sterile workers, 2.6% had better developed ovaries than spring foundresses and over 20% had at least the equivalent of one fully developed oocyte whereas an additional 20–30% may have been capable of overwintering as gynes. Ovarially developed workers were larger than those that remained sterile. Sixteen to 28% of the late summer workers were mated, but mated individuals were not more likely to have developed ovaries or to be larger than unmated bees. We discuss these findings in the light of the climate of the study area and compare this species with other members of its subgenus.

Detailed assessment of the social organisation of halictine bees requires painstaking field observations and nest excavations over the course of several flight seasons. Nonetheless, useful information can be obtained from less detailed analyses. Because of the evolutionary lability of sociality in these bees, even comparatively superficial data can be of utility in terms of plotting presence or absence of sociality upon a phylogeny or in obtaining estimates of sociobiologically important variables such as levels of morphological and physiological caste differentiation (e.g. Dunn et al. 1998).

The subgenus *Seladonia* (of the genus *Halictus*) contains species that are primarily solitary, such as *H.* (*S.*) *virgatellus* Cockerell (Eickwort et al. 1996), some with weak eusociality (Michener's 1974 terminology for social categories is used herein) as in *H. confusus* Smith (Dolphin 1971) to others with the largest colony sizes ever recorded for a halictine - *H.* (*S.*) *lutescens* Friese (Sakagami and Okazawa 1985) or the largest morphological caste differentiation – *H.* (*S.*) *lanei* Moure (Janjic and Packer 2001). However, it should be cautioned that data for these, and most other species in the subgenus, are mostly fragmentary.

Halictus (*Seladonia*) *tripartitus* Cockerell is a halictine for which the only sociobiological data available are i) the surprising observation that, at a nest aggregation, smoke blown down one nest entrance came up out of the other entrances, demonstrating that the nests were connected underground (Eickwort personal communication 1988) and ii) a statement that the species is solitary (Amdam et al. 2006). It is a somewhat divergent member of the subgenus, forming the sister group to the remainder (Danforth et al. 1999), probably along with two rare species, *H. harmonius* Sandhouse and *H. pinguismentus* Janjic and Packer (Janjic and Packer 2001, Janjic and Packer unpublished data).

For a halictine population with an archetypal eusocial phenology (and indeed other annual eusocial insects in temperate climates), only mated and comparatively unworn females are expected to survive the winter. In spring they establish nests, their wings and mandibles increase in wear and their ovaries become well developed as they produce a brood composed primarily of worker females. Individuals in this brood are usually smaller than their mother and have reduced levels of ovarian development and a low frequency of mating (partly dependent upon the availability of males produced in the "worker" brood). Depending upon the length of the flight season, additional broods, primarily of workers, may be produced. Towards the end of the colony cycle, a brood composed of males and next year's colony foundresses is produced. Much of the variation in these parameters can, to some extent, be estimated from field collected samples in the absence of nest excavations (Dunn et al. 1998). In this paper we present some phenological and social organisation data for *H. tripartitus* based upon field samples, in order to add to the intensity of taxonomic sampling for such data in these behaviourally diverse bees.

MATERIALS AND METHODS

Sampling.—*Halictus tripartitus* adults were collected on the Kunde Wine Estate, 2.3 km southeast of Kenwood in Sonoma County, California, USA (38°24'15N, 122°31'43W). This site is a low-elevation, gently sloping oak woodland dominated by blue oak (*Quercus douglasii*), adjacent to a large vineyard. The oak woodland consists of 4–10 m tall trees that are generally widely spaced with few shrubs interspersed among them. At the site, a 100 m^2 sampling plot was established.

Bees were sampled in 2002 and 2003 on clear, low wind days. As preliminary data and previous monitoring studies show that different colored pan traps attract different species of bee (Leong and Thorp 1999), the bee fauna was surveyed using a recently developed standard protocol which utilizes a mix of sweep-netting and pan trapping (protocols can be found at <http://online.sfsu.edu/~beeplot.>). Pan traps were set out between 09:00 and 15:00 and sweep-netting was done for one hour in the morning and one hour in the afternoon per sampling day.

Some samples of females from 2003 were preserved in 70% alcohol and this permitted dissection for sociobiological data (see below). All samples collected in 2002 were pinned so only phenological data could be obtained from them.

Sociobiological Data.—The preserved bees were observed under a microscope to evaluate alar and mandibular wear (based upon the right hand side), measure head width, and dissect females for insemination and ovarian development status following slight modifications of standard protocols (Ordway 1965, Abrams and Eickwort 1980). Mandibular wear was scored on a scale from 0 – completely unworn, apex sharp; to 6 – mandible worn away to the base of the subapical tooth. Wing wear was assessed by counting the number of nicks in the wing margin, completely abraded wings were scored as having 15 nicks – the number that seems to result in complete abrasion of the margin. Total wear was calculated by adding the scores for wing and mandibular wear. It is useful to exclude freshly emerged adults from some analyses, such as of ovarian development and mating, because they may not have had enough time to mate or develop their ovaries. Consequently, in many analyses only bees with a total wear score greater than one were considered. Comparisons of ovarian development among samples were performed with bees parasitized by conopids removed from the sample. In later samples, when a mixture of ageing workers and newly emerged gynes might be expected, putative examples of the latter were assumed to have

a total wear of at most one and to have entirely undeveloped ovaries. Individuals with a total wear of three or more and with completely undeveloped ovaries were assumed to be permanently sterile workers in these samples. This protocol seemed appropriate in this study as these bees appear to become worn rather slowly, their wings seem to become "nicked" particularly slowly.

The spermatheca of each bee was observed for sperm, which make the otherwise glassy-transparent spermatheca opaque. On the few occasions when there was uncertainty as to whether a bee had mated or not, the spermatheca was gradually squashed between a cover slip and a microscope slide under high magnification to look for spermatozoa. Ovarian development was evaluated by estimating the proportion of a fully developed oocyte present in the bees and summing them across the 6 ovarioles. Bees with developed ovaries (defined as with at least one ovariole with at least one quarter of a fully developed oocyte) are sometimes referred to as OD+ in the account that follows, bees without ovarian development are referred to as OD−. Caste size dimorphism is estimated as (q–w)/q where q is mean putative queen head width and w is mean putative worker head width.

Climatic data.—Because weather variation, both within and among years, influences sociobiological parameters for sweat bees (Richards and Packer 1995), we report temperature and rainfall data for the study area both in terms of data from the period when bees were sampled and for longer term average conditions. Data were taken from the Santa Rosa Airport Weather Station as indicated on the following webpages: http://www.pressdemocrat.com/nbwx/srweather/index.cfm and http://www.wunderground.com/history/airport/KSTS/1993/3/1/MonthlyHistory.html# calendar. Data presented here are for mean daily temperature and rainfall for the months of March through August 2002 and 2003, along with averages and maxima and minima for the same months over the 10 year period 1992–2001.

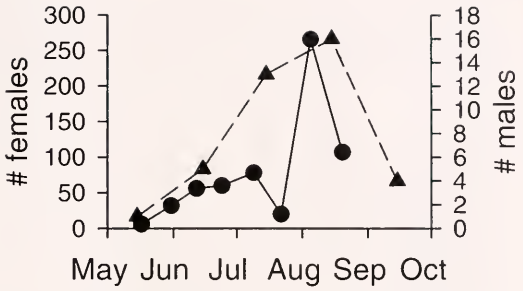

Fig. 1. Phenology of *H. tripartitus*. The left-hand axis indicates the number of females (●) while the right axis shows the number of males (▲), all collected in 2002.

RESULTS

Phenological Patterns.—During the May-September period, 2002, a total of 765 *H. tripartitus* were collected at the Kunde Wine Estate. Of these, 726 were females and 39 were males. Numbers of *H. tripartitus* females increased gradually, nearly at a constant rate, from May to mid-July (Fig. 1) peaking at the beginning of August after a temporary decrease in sample size, and then decreased rapidly until the end of the season. Males show a similar pattern, but peak in the sampling period after the females. The discrepancy between the number of males and number of females in the samples is surprising; even at the peak of male abundance, there are approximately 8 times as many females as males. Based upon observations of museum holdings, this ratio would seem not to be an artefact as males of *H. tripartitus* are rare in collections (Packer unpublished observations).

The alcohol preserved material demonstrates that the species is active as early as March (see below), and inspection of museum holdings shows that a few females can be found as late as October (Packer unpublished observations).

The March 28th sample of dissected bees suggest that nest initiation had only just begun at this time: only 39% of the bees

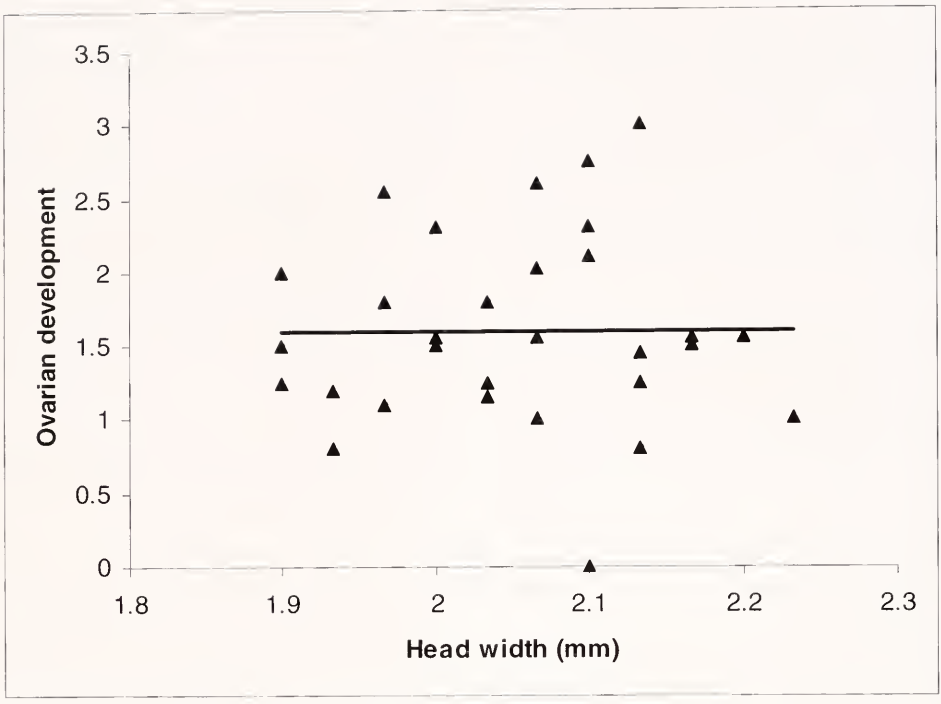

Fig. 2. Ovarian development and size variation in females of the May sample.

had mandibular wear, 16% had wing wear and 34% of them had some ovarian development with mean summed oocyte fractions of 0.16 per individual (Table 1). There was no size difference between ovarially developed and undeveloped females (mean head width OD+ females = 2.04 mm, SD = 0.11, n=54; OD− females head width = 2.06 mm, SD = .093, n= 28; t =0.93, ns). Almost all females mated (97.2%), both unmated females were above average size for the sample.

In contrast, the May 16th sample was entirely of mated bees with worn mandibles, 94% had worn wings and all except a parasitized individual had developed ovaries with the summed fractions of developing oocytes averaging over 1.6 per bee. Ovarian development was independent of bee size (Fig. 2). The mean size of March and May sample bees was 2.04 (SD = 0.10) and 2.05 mm (SD = 0.09) respectively, not significantly different ($t = 0.35$, $p > 0.5$).

Table 1. Summary sociobiological data by sample date.

Sample date	N	% of ♀ with mandible wear	% of ♀ with wing wear	% of ♀ mated	% of ♀ with* developed ovaries	Mean ovarian score*	Mean ♀ Head width
March 28	82	39	16	97.2	34	0.16	2.04
May 16	31	100	94	100	100	1.6	2.05
June 20	67	81.5	26	13.8	43	0.4	1.93
June 30	50	96	62	6.5	26	0.14	1.94
July 18	166	68.7	70.5	13.7	55	0.44	2.01
August 20	118	56	36.2	34.2	34.5	0.28	2.01

*Parasitised females omitted from ovarian development data.

The two samples from June show an increased variance in wear but decreased ovarian development in comparison to the May sample. On June 20th, 81.5% of the bees had worn mandibles, 26% had worn wings, 43% had developed ovaries and 13.8% were mated. This was the only sample in which unworn bees were significantly less likely to have developed ovaries ($\chi^2 = 7.18$, $P < 0.01$; all other samples $p > 0.16$), suggesting that many of these individuals were young and had not had time to develop their ovaries. Nonetheless, worn bees with undeveloped ovaries made up 46.5% of this sample. On June 30th comparable data are: 96% with worn mandibles, 62% with worn wings, 26% with developed ovaries (31% if only worn bees are included) and 6.5% were mated. These data suggest increased average age/activity levels of the bees over the intervening ten days but a decrease in ovarian development. The average sum of fractions of oocytes shows the same decrease over time, the values were 0.40 for June 20th and 0.14 for June 30th. Of all June bees combined, only one individual (ie < 1%) had more enlarged ovaries than the average individual in the May sample.

Ovarially developed worn bees were significantly larger than worn OD− bees in the June 30th sample (mean head width OD+ bees = 1.98 mm, SD = 0.076, n = 11; OD− = 1.92 mm, SD = .089, n = 28; t = 2.1, p< 0.05), but not in the June 20th one (OD+ = 1.95 mm, SD = 0.94, n = 23, OD− = 1.93 mm, SD = .096, n = 19; t = 0.91, ns). The proportion of bees that were mated did not differ between the two June samples (Fisher's exact test, p = 0.35).

The data suggest that these early summer bees are offspring of the generation sampled in March and May and that they represent a worker brood. The pattern of ovarian development and age in these bees suggests that more workers initiate ovarian development soon after eclosion than manage to maintain developed ovaries a short while later. Furthermore, the data indicate that individuals that do maintain developed ovaries, are disproportionately larger than those that do not.

Bees in the two June samples did not differ in size (1.93 mm and 1.94 mm for June 20th and June 30th respectively). Three individuals collected in June were extremely worn, (wing margin completely abraded), suggesting that they may be ageing overwintered females, perhaps from multiple foundress associations. All three were mated, one was parasitized with a conopid larva (Diptera, Conopidae), one had no ovarian development, the remaining individual had ¾ of a developed oocyte. Inclusion of these individuals in the comparison of ovarian development data between worn and unworn bees did not alter the statistical patterns noted above.

The July 18th sample had a lower proportion of bees with mandibular wear than in June (68.7%), a higher proportion with worn wings (70.5%) and a higher proportion with developed ovaries (55%, 54.4% when only worn bees are included). Similar to the June 20th sample, 13.7% of females were mated. The wear differential between mandibles and wings suggests that bees at this time are performing relatively more foraging or less digging than in the earlier samples. The average sum of fractions of oocytes was 0.44 and 6 individuals (3.8%) had more ovarian development than the average overwintered female in May. Worn OD+ bees were significantly larger than worn OD− bees (head width OD+ = 2.02 mm, SD = 0.07, n = 82; head width OD− = 1.98 mm, SD = 0.09, n = 44 respectively; t = 2.56, p < 0.05). Overall, July bees were intermediate in size between the smaller June and larger earlier samples, averaging 2.01 mm in head width; the sample of six individuals with very well developed ovaries had exactly the same average head width as the rest of the sample.

On August 20th the proportion of bees with worn mandibles decreased to 56% while 36.2% had worn wings. The pro-

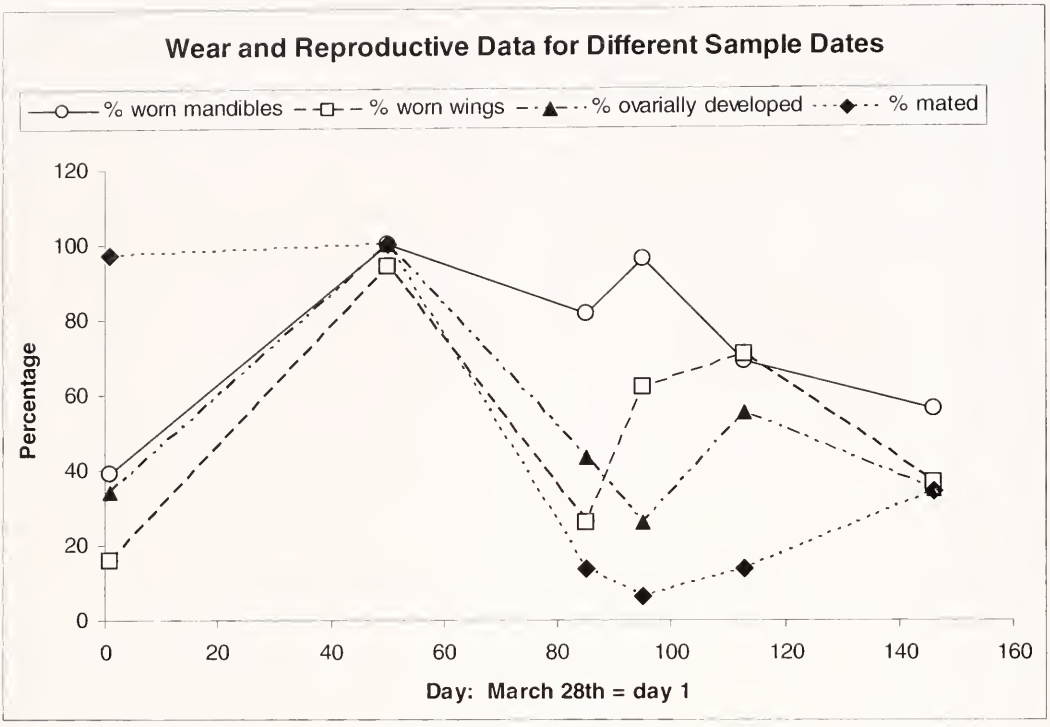

Fig. 3. Wear and reproductive variables for each of the samples of bees dissected.

portion with developed ovaries decreased to 34.5% (38.5% when only worn bees are included) and the percentage of females that had mated increased to 34.2%. The summed fraction of oocytes declined to an average of 0.28 and only one individual (<1% of the total) had ovaries that exceeded the average ovarian development of the May sample. As with the July sample, worn OD+ bees in August were significantly larger, on average, than OD− individuals (head width OD+ = 2.04 mm, SD = 0.10, n = 38; head width OD− = 1.99 mm, SD = 0.12, n = 28 respectively; $t = 2.73$, $p < 0.01$). Overall, the bees collected in August had an average head width of 2.01 mm, the individual with very well developed ovaries had a head width of 2.07 mm (not significantly larger than the sample as a whole, Mann Whitney U test, $p = 0.65$).

The wear and reproductive data discussed above are shown visually in Fig. 3.

Size variation among the four samples (March and May samples combined, two June samples combined) is significant (ANOVA, $F = 6.0$, $p = 0.0005$). Tukey's HSD test reveals that this result is due to the June bees being significantly smaller than the others ($p<0.01$ for the overwintered female comparison and $p<0.01$ and $p< 0.05$ for the comparisons with July and August samples respectively).

Caste.—The data above are consistent with the March sample consisting of overwintered females at the nest initiation phase, the May sample comprising the same generation individuals actively provisioning nests and with the June sample being first brood workers. The three heavily worn June bees perhaps represent subordinates in multiple foundress associations. Although this would require nest excavation data for confirmation, it is uncommon for solitary foundresses to forage for such an extensive period of time

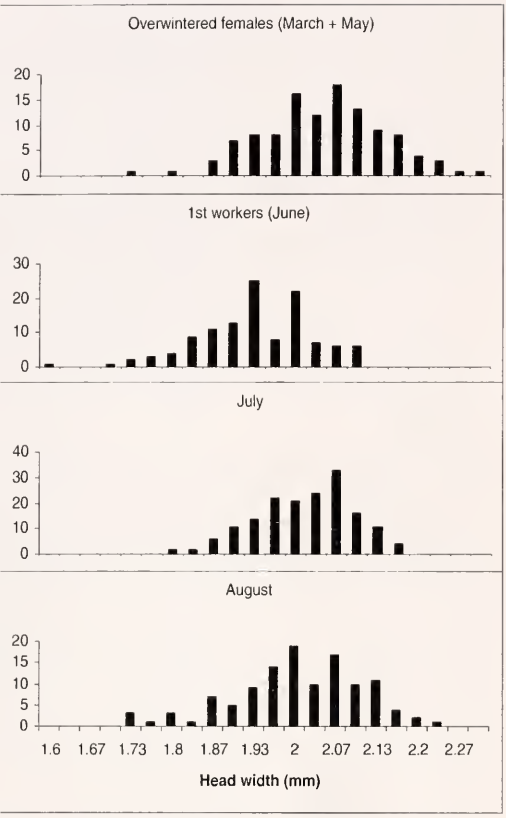

Fig. 4. Size variation (head width) among females from each of the months sampled.

or to become so heavily worn. If this is the case, then the putative gynes average 2.04 mm in head width (SD = 0.10) and the first worker brood 1.94 mm (SD = 0.09), the castes differ significantly in size ($t = 11.22$, $p << 0.001$) and the morphological size difference between gynes and the first worker brood is 5.14%.

Size variation data for the overwintered females, first brood workers and July and August females are shown in Fig. 4.

July and August females are not so easily categorised as to caste as they are expected to include some newly emerged gynes as well as ageing workers and perhaps some young workers also. We take ageing bees with undeveloped ovaries to be sterile workers, ageing bees with well developed ovaries (with total ovarian development at least equivalent to one fully developed oocyte) to be potentially reproductive workers and unworn bees with completely undeveloped oocytes to potentially be gynes.

Data for these three groups are shown in Table 2 separately for July and August. Interestingly, the sizes of the potential gynes in July are very similar to those for the overwintered females the previous March and May. The reproductive workers are also somewhat large, but their wear indices suggest that they do not represent the same overwintered females as were sampled in March and May as their index of wear is too low for them to have been active for the entire intervening period (only three of 40 have a higher index of wear than the average female in the May sample) and none of them are mated. The sterile workers are the smallest individuals in the sample.

The pattern for the same three classes of bee for the August sample is quite different. In August the sterile worker and potential gyne samples are identical in size but the reproductive workers are larger. Indeed, the mean size of the reproductive workers in August is the largest of any of the categories analysed in any time period. Even these, however, would not seem to be remaining overwintered females as only 4

Table 2. Sociobiological data for different "castes" of summer female. For explanation of caste designation see text.

	July		August	
Putative Caste	Head width (SD) N	% mated	Head width (SD) N	% mated
Sterile workers	1.99 (0.07) 22	13.6	1.99 (0.09) 10	60.0
Reproducing workers	2.02 (0.09) 5	0.0	2.10 (0.14) 5	0.0
Gynes	1.99 (0.09) 30	28.9	2.03 (0.08) 45	17.4

of the 15 have a total wear greater than the May sample and none of them are mated.

It would seem that the fates of bees eclosing in summer are highly variable. Some seem to remain strictly as workers, attaining high wear indices without developing their ovaries. A total of 55% of the July and August bees had a total wear index of 3 or more but had completely undeveloped ovaries. Such bees were smaller than the worn bees that had developed ovaries and the size difference between these apparent permanent workers and their contemporaries that have highly developed ovaries, with ovarian development greater than or equal to one is even larger: 3.8% ($t = 5.24$, $p << 0.001$) and 4.8% ($t = 4.54$, $p << 0.001$) for July and August samples respectively.

For none of the samples of worn bees was there a significant association between ovarian development and mating ($p > 0.5$ in all comparisons). Similarly, the mated bees were not larger than unmated ones (worn bees only) in any of the analyses ($p > 0.5$ in each case) except for the July sample in which the mated bees were significantly larger than the unmated ones (head width mated = 2.05 mm, SD = 0.08, $n = 14$, head width unmated = 1.99 mm, SD = 0.06, $n = 75$; $t = 7.14$, $p << 0.001$).

Parasitism.—One female was found with a large nematode in the metasoma, she was from the March sample of overwintered females. Twenty females were parasitized with one conopid larva in each metasoma and three contained two parasite larvae. It is likely that these parasitism rates are underestimates as small conopid larvae and nematodes would likely have been missed in the dissections, especially if they were primarily underneath the first metasomal tergum, which was not removed.

Of the 23 females with conopids, one was found in the May sample, four each in the two June samples, eight in July and six in August. The overwintered females were significantly less affected by conopids than were later females (Fisher's exact test $p = 0.0377$). The long period during which conopid larvae were found suggests either that the parasite has more than one generation per year, or that multiple species of conopid are involved.

Bees with conopid larvae did not differ in size from the other individuals in their samples ($p > 0.2$ in all cases), but they did have more wear than their contemporaries in July and August (Mann Whitney U test, $U = 991$, $p = 0.007$ and $U = 536$, $p = 0.014$ respectively) but not in either of the June samples ($U = 191$, $p = 0.059$ and $U = 130$, $p = 0.187$).

Climate and Weather.—The collection period for *H. tripartitus* was from May to August 2002 for the pinned specimens and from March to August 2003 for the pickled ones. The weather data for the months March to August are shown in Fig. 5 along with averages for the previous ten year period. 2002 was drier, but 2003 was wetter than the average for the previous ten year period. In both years April was an extreme month, with more than double the average rainfall in 2003 and less than a quarter the normal amount in 2002. The temperature data show that 2002 varied little from the average conditions whereas in 2003 April was cooler than any year between 1992 and 2002 and July was warmer than in any of these other years.

DISCUSSION

Halictine bees are well known for their variable social behaviour, not only within and between populations and species but also among individuals within a colony. Taken in their entirety, our data strongly support the view that *H. tripartitus* is primarily eusocial at our study site. Perhaps the strongest evidence for this comes from all overwintered females being mated whereas the first brood offspring were almost entirely unmated. Indeed, as a whole, the data are mostly consistent with the view that this species is a typical annual eusocial species with overwintered females initiating nests in March and

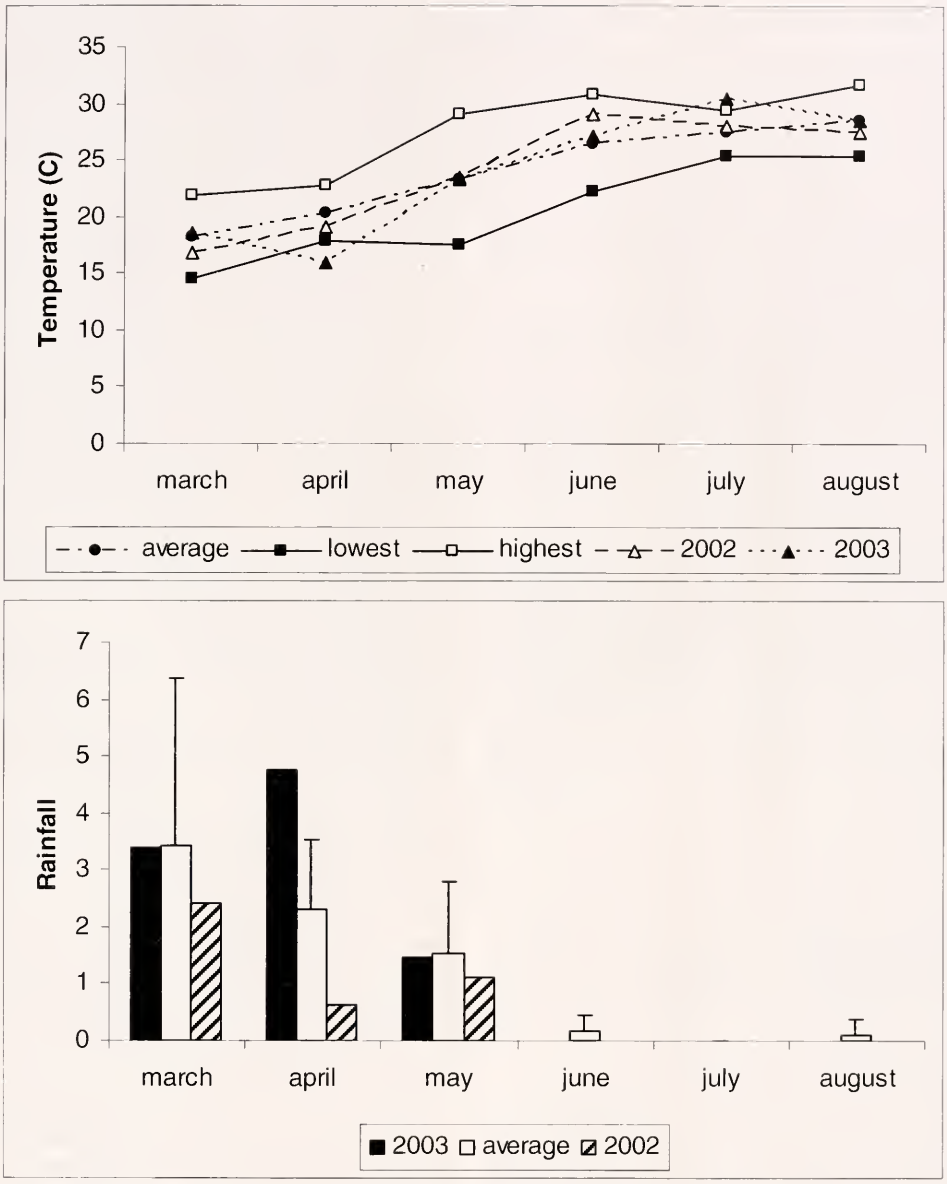

Fig. 5. Weather data for 2002, 2003 and summaries for the ten previous years 1992–2001.

foraging until May, workers emerging in June and overwintering gynes commencing emergence in July. Less usual features are the apparent multiple nest entrances, low frequency of males and the nature of the sample in August. We return to these three aspects towards the end of the discussion after considering worker fitness options and making comparisons between *H. tripartitus* and other species of the subgenus *Seladonia*.

Fitness options for bees eclosing in summer within a eusocial family structure include remaining as a sterile worker, attempting to produce some offspring directly or initiating a nest either the same year as they eclose (Richards et al. 2003) or after overwintering (Yanega 1988). Given

the Mediterranean climate of the region and the dryness and hardness of the soil in summer, initiating a nest in summer is probably not a very profitable option (McCorquodale 1989). Furthermore, as the most ovarially developed summer bees were unmated, it is unlikely that they are founding new nests at this stage, unlike some summer females of *Halictus* (*Halictus*) *sexcinctus* (Richards et al. 2003).

Halictus tripartitus worker brood individuals seem to take advantage of at least three of these options. Of the July and August samples, approximately 55% seem to be sterile workers and perhaps 20% of them seem capable of reproducing. Over 2% of the bees collected in July and August had ovaries more fully developed than did the foundresses in spring, suggesting that either some are nesting solitarily or they have the potential to reproduce in their natal colony (as has been demonstrated using genetic markers in several other species, Packer and Owen 1994, Richards et al. 1995). As none of these most ovarially developed later workers were mated, the offspring they produce must be male. However, few males are ever seen in this species. This would be in agreement with Packer and Owen (1994) where genetic data showed that considerable levels of ovarian development resulted in few instances of successful oviposition by workers of *Lasioglossum laevissimum*.

The fourth option, mated worker brood females overwintering and initiating a nest the following spring, cannot be confirmed or refuted with the data at hand. It remains possible that brood divalency may occur in *H. tripartitus*. The easiest way to document this would be to mark large numbers of emerging "worker" brood females as they leave the nest and search for them when the foundresses begin activity the following spring.

Few species of the subgenus *Seladonia* have received detailed sociobiological investigation. The best studied is *H. (S.) hesperus* Smith, which has large colonies and very large morphological caste differentiation with concomitantly low worker ovarian development (<1% of workers seemingly capable of reproduction, Brooks and Roubik 1983, Packer 1985). *Halictus (S.) lutescens* has even larger colony sizes and in the one nest excavated by Sakagami and Okazawa (1985) approximately one quarter of the workers seemed capable of reproduction, though it remains likely that this colony was studied after the death of the queen. A third species, *H. (S.) lanei*, has the largest caste size dimorphism of any halictine known (Janjic and Packer 2001), although its social organisation may not fit the standard eusocial model (Gravel et al. in preparation). All three of these species are tropical and their workers seem not to have the range of options that may be available to *H. tripartitus*. In contrast, the alpine *H. (S.) virgatellus* is predominantly solitary with a few nests being shared (Eickwort et al. 1996). The north temperate *H. (S.) confusus* and its sibling species *H. (S.) tumulorum* (L.) are weakly eusocial, perhaps reverting to solitary behaviour at the northern edge of their ranges (Dolphin 1971, Sakagami and Ebmer 1979). Worker brood individuals in these species likely have a similar range of options as suggested above for *H. tripartitus*, albeit usually within a shorter summer activity period, but appropriately detailed studies remain to be published.

Richards and Packer (1995) found that variations in local weather patterns affected the demography and behaviour of *H. (H.) ligatus* colonies: warmer and drier weather resulted in larger broods with better survival rates and lower nest-failure and more reproduction by workers. Thus, warm, dry weather resulted in weaker eusociality. Conversely, colder, wetter conditions gave rise to smaller workers with greater reproductive differentiation between the castes but also lower brood-survival rates and more nest-failure. Colder and wetter weather resulted in stronger eusociality. The area where *H.*

tripartitus was studied was unusually cold and wet in April of 2003, during foundress provisioning. If the weather influences this species in the same manner as it does with *H. ligatus*, it is likely that early summer colonies were smaller, with stronger physiological caste differentiation than is usual for this population. The poor weather in April may also explain the apparently extended period of activity of overwintered foundresses.

There are no detailed studies of social sweat bees from Mediterranean climates in North America. The restriction of precipitation to the winter and early spring is a feature that can limit the duration of colonies of social bees in the area and few individuals of *H. tripartitus* have been collected from late August onwards: even though temperatures are adequate for activity, the dry conditions severely restricts the availability of forage. It is likely that the late summer activity of this species is a comparatively recent phenomenon as at this time of year they rely upon flowering of plants that are maintained by agricultural irrigation. This could explain the unusual nature of the August sample.

Two other unusual aspects of this species' biology are worthy of comment, and may be related. First, the very low proportion of males, either as sampled here or in museum collections, is surprising. Towards the end of the colony cycle in most eusocial halictines, males are approximately as common as females, yet in *H. tripartitus* they are almost an order of magnitude less common. Second, the observation of nests apparently being connected underground is entirely unique among bees. It remains possible that males primarily search for mates underground, thereby uniting these two unusual phenomena. Certainly this species is worthy of more detailed field investigations, something we hope this paper will stimulate.

Lastly, the observation that worker ovarian development seemed to decline over time is of interest. This phenomenon has been observed in numerous social insects. There are two main reasons this might be the case. First, the act of work might make it less likely that a bee has the energy resources to develop oocytes – which are remarkably large in comparison to bee body size in halictines. Alternatively, it could be that workers develop their ovaries primarily to coincide with male production when reproductive broods are protandrous. The fact that first brood workers are active at a time of year when few males are being produced in *H. tripartitus*, argues against the second explanation.

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The Status of *Liris magnificus* Kohl, 1884, and *Trachogorytes costaricae* R. Bohart, 2000 (Hymenoptera: Crabronidae: Crabroninae, Bembicinae)

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Abstract.—The Australian *Liris magnificus* Kohl, 1884, currently treated as a subspecies of *Liris haemorrhoidalis* (Fabricius, 1803) from the Palearctic and Afrotropical Regions, is an independent, full species. The taxonomic history of the species is reviewed and the differences with *haemorrhoidalis* are discussed. *Trachogorytes* Bohart, 2000, a monotypic genus described for *Trachogorytes costaricae* Bohart, 2000, is actually a junior synonym of *Mellinus* Fabricius, 1790. *Mellinus costaricae* Bohart, 2000, comb. nov., is redescribed.

Liris magnificus Kohl

Liris magnificus Kohl, 1884:356, E (as *magnifica*, incorrect original termination). Holotype or syntypes: E, northern Australia: no specific locality (Naturhistorisches Museum Wien). – Kohl, 1892:228 (in key to world *Liris* s.s.); Turner, 1908:473 (as new synonym of *Liris haemorrhoidalis*); Dollfuss, 1989:10 (type material in NHMW). – **As *Larra magnifica***: Kohl, 1885:245 (new combination, in checklist of world *Larra*); Dalla Torre, 1897:669 (in catalog of world Hymenoptera). – **As *Liris haemorrhoidalis magnifica***: Williams, 1928:49 (new status, nesting habits); Bohart and Menke, 1976:245 (as tentative subspecies of *Liris haemorrhoidalis*); Cardale, 1985:235 (in catalog of Australian Sphecidae); Naumann, 1993:185 (Australia: Queensland: Heathlands area in Cape York).

Liris magnificus was described as a full species, but was synonymized with *haemorrhoidalis* (Fabricius) by Turner (1908). Surprisingly, the author stated "I cannot detect any appreciable difference in the male", but in fact the males are strikingly different (see below). Both species, however, are similar in having a non-emarginate posterior mandibular margin, red legs, and conspicuously golden body setae, a combination unique within the genus. Williams (1928) treated *magnificus* as a subspecies of *haemorrhoidalis*, an interpretation followed by Cardale (1985) and Naumann (1993). Bohart and Menke (1976), on the other hand, regarded the subspecific status of *magnificus* as tentative.

Having recently examined five females and six males of *magnificus*, I conclude that it is actually a full species, and not a geographic form of *haemorrhoidalis*. The differences between them are as follows. In *magnificus*, the median swelling of the pronotal collar is wider (Fig. 2b); in the female, the carina emerging from the clypeal lobe corner is about twice as long as the midocellar width (Fig. 2a) and the dark apical coloration of fore wing does not extend into the cell area (Fig. 2c); the male hind tarsomere II is simple, as in most of the congeners; in most males the hind coxa is concave ventrally and carinate along inner margin (Fig. 2d), but slightly convex ventrally and obtuse along inner margin in one specimen from Wonga Beach. In *haemorrhoidalis*, the median swelling of the pronotal collar is narrower (Fig. 1b); in the female, the carina emerging from the clypeal lobe corner is about as long as midocellar width (Fig. 1a) and the dark apical area of fore wing covers marginal as well as second and third submarginal cells (Fig. 1c); in the male the

Fig. 1. *Liris haemorrhoidalis* (Fabricius): a – lateral carina of female clypeal lobe in oblique view; b – female pronotum; c – apical half of female fore wing; d – male hind tarsomere II.

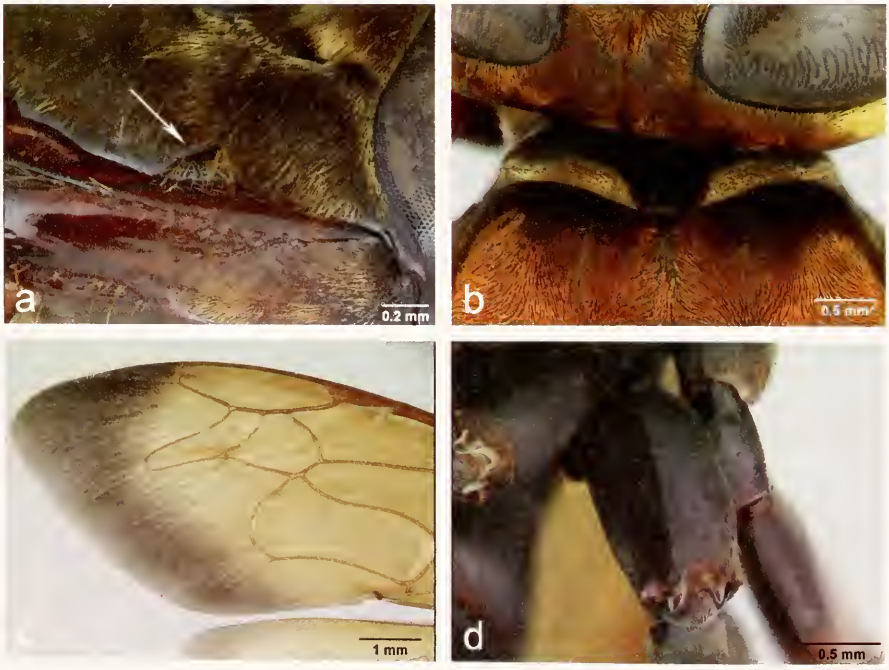

Fig. 2. *Liris magnificus* Turner: a – lateral carina of female clypeal lobe in oblique view; b – female pronotum; c – apical half of female fore wing; d – male hind coxa.

hind coxa is neither concave nor carinate, and hind tarsomere II is conspicuously expanded (Fig. 1d), a unique such feature in the genus. The genitalia appear identical in both species. The two species do not occur sympatrically: *Liris magnificus* is known only from Australia, whereas *haemorrhoidalis* occurs throughout Africa, Spain, the Canary Islands, and southwestern Asia to western India and Sri Lanka.

Records (all specimens are at the California Academy of Sciences).—AUSTRALIA: **Queensland**: Armstrong Beach ca 15 km E Sarina at 21°27.3′S 149°17.5′E, 29 Oct. 2006, W.J. Pulawski (1 ♂); Balgal Beach 51 km NW Townsville at 19°02.5′S 146°25.2′E, 18 May 2007, V.E. Ahrens and W.J. Pulawski (1 ♀); Blacks Beach ca 8 km N Mackay at 21°03.6′S 149°11′E, 1 Dec 2006, W.J. Pulawski (1 ♂); Burdekin River 20 km NE Charters Towers at 20°00.1′S 146°26.3′E, 26 Nov 2006, W.J. Pulawski, and 21–22 May 2007, V.E. Ahrens and W.J. Pulawski (1 ♀, 1 ♂); Crystal Cascades 10 km W Cairns, 9–10 July 1983, T.W. Davies (1 ♀); 69 road km WNW Mount Carbine at 16°13.2′S 144°43.8′E, 13 May 2007, V.E. Ahrens and W.J. Pulawski (1 ♀); Wonga Beach 11 km NNE Mossman at 16°19.9′S 145°25.3′, W.J. Pulawski, 19 Nov 2006 (1 ♀, 1 ♂) and 21 Nov 2006 (1 ♂).

Mellinus costaricae (R. Bohart, 2000), new combination

Trachogorytes costaricae R. Bohart, 2000:168, ♀. Holotype: ♀, Costa Rica: Puntarenas: San Vito (University of California, Davis). – Amarante, 2002:19 (in catalog of Neotropical Crabronidae).

R. Bohart (2000) published an important revision of the Neotropical Gorytini in which he described eight new genera and a number of new species. One of them was *Trachogorytes costaricae*, based on a single female from Costa Rica. I have examined that specimen and found that it is a member of *Mellinus* based on the wing venation (second submarginal cell not receiving any of the recurrent veins), non-emarginate posterior mandibular margin, short tongue, absence of an omalus and oblique scutal carina, raised and well separated pronotal collar, scutellum, and metanotum, evident

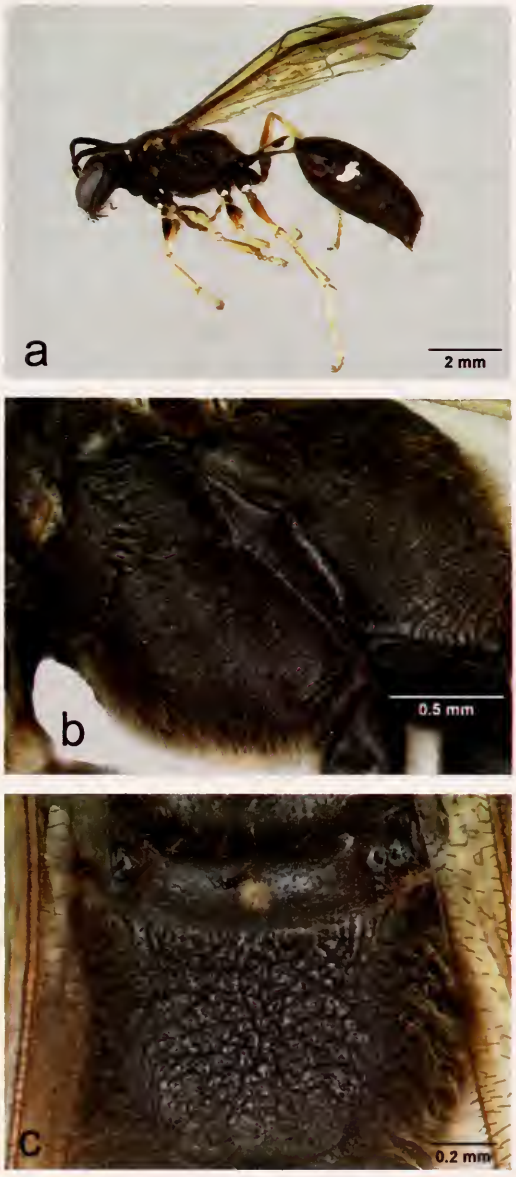

Fig. 3. *Mellinus costaricae* (Bohart), holotype: a – whole body in lateral view; b – mesopleuron; c – propodeal enclosure.

notaulus, propodeal dorsum with well-defined enclosure, submarginal cell III long and distally acute, mid-coxa simple, presence of two mid-tibial spurs, and a pedunculate gaster (Bohart and Menke 1976).

In Menke's key (1996) to Neotropical *Mellinus*, this species runs to *henseni* Menke. It differs from *henseni* and all other currently

recognized *Mellinus* (Siri and Bohart 1974, Menke 1996) by its unique sculpture: the mesopleuron is longitudinally ridged in the posterior half (Fig. 3b) rather than punctate or uniformly microsculptured, the propodeal enclosure is all coarsely rugose (except at the very apex), the propodeal side is longitudinally ridged, and the propodeal posterior surface is rugose (Fig. 3c), not punctate, as stated in the original description. Additionally, the tentorial pit is closer to the antennal socket than to the eye margin and the propodeal side is separated from the posterior surface by a conspicuous carina, as in the Palearctic *arvensis* (Linnaeus) and *crabroneus* (Thunberg). Most of the body is black (Fig. 3a), but the following are whitish: narrow paraorbital strip in the ventral half of the frons, clypeus (except along frontoclypeal margin), scape ventrally, mandible (except apically), mesally interrupted fascia on pronotal collar, pronotal lobe apically, anterior half of tegula, tiny median spot on metanotum, tergum I laterally (except in basal half) and apically, and a pair of preapical, widely separated spots on tergum II. The femora are blackish basally, then reddish brown and yellow; the tibiae are reddish brown and yellow; and the tarsi are yellow.

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Interspecific Variation in Hunting Behavior of *Pepsis grossa* (Fabricius) and *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae): A field study

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Abstract.—Field studies were conducted on encounters between the spider wasps *Pepsis grossa* (Fabricius) and *P. thisbe* Lucas, and females of their host spider, *Aphonopelma steindachneri* (Ausserer) (Theraphosidae), in Big Bend National Park, Texas. Females of *P. grossa* were significantly larger than those of *P. thisbe*. Number of eggs found in ovarioles of *P. grossa* and *P. thisbe* ranged from 6–14 and 3–12, with a mean of 11.3 and 8.4, respectively. Behavioral acts comprising hunting behavior of both species included antennation of a spider's burrow (BA), evicting spiders from their burrow (EVB), initial approach and antennation of spider (AA), moving away and grooming (MG1), attack and paralysis (AP), moving away/grooming (MG2), drinking behavior (DB), burial of spider and egg deposition (BO), and closure of the burrow entrance (BC). Antennae of most wasps made initial contact with the forelegs or palps of a spider. During AP, wasps typically grasped leg 3 or 4 of the host before inserting their stings. Most wasps of *P. grossa* (78%) inserted their sting into the intersegmental membrane between the sternum and coxa 2 of the spider; 88% of *P. thisbe* females chose a site between the sternum and coxa 1. Only 33 and 26% of *P. grossa* and *P. thisbe*, respectively, drank fluids from a spider's mouth or from sting insertion site (LB). *Pepsis thisbe* required significantly more time (mean: 129.1 min) to complete all behavioral acts of hunting than *P. grossa* (mean: 101.4 min). Wasps were successful in paralyzing spiders in all observed encounters, and no spider attempted to attack a wasp.

Aculeate spider wasps of the genus *Pepsis* (Hymenoptera: Pompilidae) include at least 133 species varying in size from >60 mm to <12 mm in length (Vardy 2000). Most members of this genus have been referred to as tarantula hawk wasps because females selectively hunt mygalomorph spiders of the family Theraphosidae (Cazier and Mortenson 1964, Punzo and Garman 1989, Vardy 2002). They paralyze and store these spiders (hosts) in underground nests (Williams 1956, Punzo and Ludwig 2005) as a food source for their carnivorous larvae (Punzo 1994a). They occur throughout the New World, from the United States and West Indies, south to Patagonia (Hurd 1952, Vardy 2000).

Pepsis grossa (Fabricius 1798) and *P. thisbe* Lucas (1895) are large, long-legged wasps and are conspicuous components of the arthropod fauna of desert regions in the southwestern United States and northern Mexico (Hurd 1952, Vardy 2000, Punzo, 1994b, 2006a). In Big Bend National Park (BBNP; Brewster County, Texas, USA), females of these two species, as well as *P. mildei* Stål (1844) selectively hunt and paralyze the large theraphosid spider, *Aphonopelma steindachneri* (Ausserer 1929) which they use as a host for their developing larvae (Punzo 2005a).

Adult wasps feed on nectar which is obtained from flowers of a variety of plants (Evans and West-Eberhard 1970, Punzo 2000, 2006a). In BBNP, where ambient temperatures in late spring and summer may exceed 43 °C, it is not uncommon for females to fly over considerable distances during daylight hours in search for flowers and host spiders (Punzo 1994b, Schmidt

2004). It is important for females to obtain adequate amounts of required nutrients because insect flight places high metabolic demands on insects (Nation 2002).

Females of *Aphonopelma steindachneri* (Ausserer), like other spiders of this genus, excavate burrows (or occupy abandoned rodent burrows) where they remain for most of their lives (Baerg 1958, Gabel 1972, Punzo 2007a). Females seize prey that approaches close to the burrow entrance. Adult males actively wander over the ground surface during the mating season when they search for conspecific females (Punzo 2000, 2007b).

Female *Pepsis* wasps initiate their search for suitable spider hosts after mating (Punzo 1994b, 2006a,b). They typically fly over the ground and are thought to detect occupied spider burrows at a distance using visual and/or odor cues. They intermittently interrupt flight by landing on the ground and walk rapidly over the surface, tapping the ground surface frequently with their antennae as they search for spider burrows (Kurczewski and Kurczewski 1968). When a suitable spider burrow is located, the female wasp typically stops at the entrance and taps the edge of the opening with her antennae (burrow antennation, BA). After a variable period of time, she cuts through the silk covering over the burrow entrance with her mandibles, enters the burrow, and usually forces the spider out of its burrow and onto the surface (EVB, eviction behavior). Male theraphosids are usually encountered as they move about searching for food and mates (Minch 1979, Punzo 2005b, 2007b). Unlike burrow-dwelling females, males of the genus *Aphonopelma* from dessert regions usually seek shelter within or under rock crevices, or under surface debris (Smith 1994, Punzo and Henderson 1999).

A specific sequence of behavioral acts are exhibited once a spider has been forced to the ground surface. These acts comprise the overall attack behavior of *Pepsis* wasps found in the tropics and desert regions of the southwestern United States (Petrunkevitch 1926, 1952, Cazier and Mortenson 1964, Punzo and Garman 1989, Punzo 1991, 1994b, 2005a,c). A female wasp typically approaches the spider and touches its body surface with her antennae (approach and antennation, AA) (Punzo and Garman 1989). In some cases, the spider does not move away, although it may twitch one of its forelegs or raise its palps off the ground (Punzo 2007b). In other instances, tactile stimulation by a wasp elicits a threat posture from the spider which elevates the anterior legs and exposes its fangs (Petrunkevitch 1952, Punzo 1994b). However, the spider rarely strikes at the wasp, although if presented with another insect (cricket, etc.) it typically strikes quickly, seizing the insect and eating it. It has been suggested that chemosensory cues associated with the wasp's cuticle inhibit the spider's strike response (Punzo 2000).

Once a spider has been identified as a suitable host, the wasp moves a short distance away and exhibits grooming behavior by passing its antennae through the mandibles. This behavioral component is known as 'moving away and grooming' (MG1, Punzo 1991). After a few minutes, the wasp turns to face its host and then walks under the ventral body region of the spider. In response to this, spiders usually extend their legs, elevating their body off the ground. The wasp then grasps one of the spider's legs and quickly inserts its sting through the ventral body region into the prosomal nerve mass resulting in a rapid paralysis of the spider. This component of hunting is referred to as attack and paralysis (AP). Once a spider is immobilized, the wasp moves away and repeats the grooming sequence described above (MG2). It then returns to the spider and in some instances may either drink fluids from the spider's mouth cavity or drink spider hemolymph that leaks out of the puncture wound made by the insertion of the sting. This is known as drinking or

lapping behavior, DB (Punzo 2000). However, because DB does not occur in most encounters, the question arises as to what factor(s) may be responsible for its occurrence.

The paralyzed host is then dragged into the spider's burrow (or one excavated by the wasp) and a single egg is deposited on the ventral surface of the spider's abdomen (burial and oviposition, BO). The wasp then closes the burrow entrance (BC, burrow closure) using soil particles and small pebbles and flies off to search for another host.

Although behavioral acts of the hunting sequence have been studied, most observations are based on laboratory encounters between wasps and hosts (Punzo 1991, 1994b, 2007). Few detailed observations of encounters in the field have been described. In addition, there are a number of questions that remain. For example, when attacking a spider does a wasp exhibit any preference for grasping a particular leg? Are there specific sites on the spider's body where a wasp inserts its sting? How commonly does lapping behavior occur? Is there a preference for the site at which it occurs? Finally, are there interspecific differences associated with these behaviors? The present study was conducted in order to analyze hunting behavior of *P. grossa* and *P. thisbe* under natural conditions and to address these questions in these two sympatric species of wasps that are found in similar microhabitats in Big Bend National Park (BBNP), where both utilize *A. steindachneri* as a host.

DESCRIPTION OF GENERAL STUDY AREA

Pepsis grossa and *P. thisbe* occur throughout Big Bend National Park (BBNP) is located in Brewster County, Texas, and lies within the northern region of the Chihuahuan Desert. Its western, southern and eastern boundaries are bordered by the Rio Grande River. Climatic conditions range from arid to semiarid, with mean monthly air temperatures ranging from 5.4 C in January to 33.8 C in August (US Dept. of Interior 2005). Annual rainfall is between 13.8–30.1 cm, depending on location and altitude, with 65–70% occurring from May through October (Parent 1996). Topography of the Park is diverse and includes gypsum formations, igneous rocks, and limestone deposits that provide different substrates including alluvial fans, gypsum flats, saline playas, siliceous and gypsum dunes, fine-textured basins, canyons, mountain ridges, and freshwater springs and seeps, all supporting a diverse plant fauna categorized within distinctive vegetative zones (Powell 1988).

MATERIALS AND METHODS

I conducted field studies over a 4-year period (2002–2005) within BBNP from May through September, when male wasps were establishing perch sites (territories) and females were searching for spiders. Adults of *P. grossa* and *P.thisbe* were observed within a 5-km radius of Tornillo Flat (TF; 29 01'N, 102 59W), a site where both of these species are abundant, as well as their host spider, *A. steindachneri*, are abundant (Punzo 2000, 2007b). I had located and marked numerous occupied tarantula burrows during previous field studies in this area over the last 12 years (n = 946). Females of *A. steindachneri* typically remain within a single burrow for most of their adult lives (Punzo, unpubl. data). As a result, I knew the locations of host spiders and concentrated my field observations at these burrow sites. Voucher specimens of wasps, wasp eggs, and spiders have been deposited in the invertebrate collection at BBNP.

Based on my knowledge of locations for burrows occupied by a female tarantula, I examined 148 burrows whose entrances had been closed from previously unobserved encounters with wasps to determine whether it contained a paralyzed host. During the course of this study I also monitored 96 burrows containing an adult

female spider, and observed 54 and 42 encounters between a wasp and spider for *P. grossa* and *P. thisbe*, respectively. Because encounters between a wasp and a male spider usually occur while the male is wandering over the ground surface, opportunities to witness such encounters occur far less frequent. Therefore, only encounters involving a female spider were used for analyses.

I observed all encounters at close range (1–2 m from combatants), and used a 35-mm Nikon FE2 camera to photograph some of the encounters. Encounters were observed during daylight and evening hours (0830–0200 h, Central Standard Time). At the end of each encounter (following burial, oviposition, and closure of the burrow) I collected the wasp with a sweep net and anesthetized it using a portable CO_2 cartridge. Once inactivated, I verified species identification and used a Unitron dissecting microscope fitted with an ocular micrometer to record body length and head capsule width. Although *Aphonopelma steindachneri* is the only theraphosid known to occur at the TF site (Smith 1994, Punzo 2007b), I opened each burrow to verify species identification of paralyzed spiders. I examined the body surface of paralyzed spiders with a dissecting microscope in order to locate the site where the wasp's sting had been inserted into the host during the paralyzation sequence. I also recorded the width of the carapace and total body length to the nearest 0.1 mm using a digital caliper. After removing the wasp's egg, I recorded weight of wasp eggs (to the nearest 0.01 mg) and spiders (to the nearest 0.01 g) using a portable electronic balance. Egg length and width were recorded to the nearest 0.01 mm using a dissecting microscope.

The site of the puncture wound could be readily identified by hemolymph that oozed out of the wound. Only data obtained for *P. grossa*, *P. thisbe* and the host *A. steindachneri* were used for analyses. Another *Pepsis* wasp, *P. mildei* also occurs at TF, but is far less abundant (Punzo, unpubl. data). After measurements were recorded, each wasp was preserved in 70% ethanol for subsequent determination of number of eggs in ovarioles. Removal of wasps ensured that the same wasp was not involved in more than one encounter for the data set.

For each encounter I observed the general behavior of the wasp as it approached the burrow entrance and interacted with a spider, as well as the concomitant behaviors exhibited by the host. I recorded: (1) the amount of time required to complete the hunting sequence (from initial contact to closure of the burrow), as well as all behavioral components of hunting, using a stopwatch; (2) which spider leg was initially seized by the wasp as it attempted to insert its sting; (3) site at which wasp sting had been inserted into the body of the spider; and (4) whether or not lapping behavior occurred, and if so, where.

All statistical procedures followed those described by Sokal and Rohlf (1995). All data conformed to conditions of normality as assessed using a Bartlett's test for homogeneity of variances and a *G*-test for normality. Comparisons on means for morphometric data between the two species of wasps as well as for male and female spiders were tested using a *t* test. Differences between the proportion of burrows containing paralyzed males versus females, and frequency at which specific spider legs were grasped by a wasp during initiation of attack behavior, were tested using a Chi Square test (X^2). Comparisons between time required by each wasp species to complete overall hunting sequence was tested using an analysis of variance (ANOVA), and a Scheffe F test was used for ad hoc comparisons between individual behavioral components of hunting.

RESULTS

Of the 148 burrows whose entrances had been closed with soil (following previously

Table 1. Morphometric data on females of *Pepsis grossa* (n = 54) and *P. thisbe* (n = 42) and female host spiders, *Aphonopelma steindachneri* (n = 96 females, 46 males) at Tornillo Flat, Big Bend National Park, Texas. Data from wasps and spiders examined from 2002 to 2005. Data expressed as means; values in parentheses represent (±SE). BL (body length); HCW (head capsule width); CW (cephalothorax width); BW (body weight); NEO (number of eggs found in ovarioles). Values in rows followed by a different letter are statistically significant (t tests; $P < 0.05$).

	Pepsis grossa	*P. thisbe*	*A. steindachneri*	
BL (mm)	42.7a (2.4)	35.9b (1.7)		
HCW (mm)	4.9a (0.2)	3.9b (0.3)		
NEO	11.3a (2.4)	8.4b (0.7)		
			Males	Females
CW (mm)			13.4a (0.7)	15.2b (0.5)
BW (g)			6.8a (0.5)	10.8b (1.1)

unobserved encounters), 128 (87%) contained a paralyzed spider. Although the species of wasp responsible for the paralysis cannot be known unless the offspring is reared, 87 of these 128 burrows (68%) contained a female spider, and 32% held a male (Chi Square test: $X^2 = 10.89$, $P < 0.03$). Paralyzed male spiders ranged in weight from 5.2–6.4 g (mean: 5.77 ± 0.42), while the range was 6.9–10.4 g (mean: 7.94 ± 0.37) for females. For data obtained from observed encounters, female spiders paralyzed by *P. grossa* and *P. thisbe* had a mean weight of 8.7 ± 0.83 g (range: 6.2–10.6) and 7.7 ± 0.64 g (range: 5.7–10.7), respectively. Mean values for length, width, and weight for eggs of *P. grossa* were 4.34 ± 0.03 mm, 1.34 ± 0.01 mm, and 7.14 ± 0.31 mg, as compared to 4.29 ± 0.05 mm, 1.24 ± 0.02 mm, and 6.88 ± 0.41 mg for *P. thisbe*.

Morphometric data for wasps observed encountering spiders, as well as for hosts, are shown in Table 1. Concerning host spiders, based on width of cephalothorax ($t = 3.04$, $P < 0.05$) and body weight ($t = 2.46$, $P < 0.05$), females were significantly larger than males. For the two species of wasps, females of *P. grossa* were significantly larger than those of *P. thisbe*, based on body length ($t = 3.35$, $P < 0.05$) and head capsule width ($t = 2.88$, $P < 0.05$).

Data on wasps collected from the field indicated that the mean number of eggs found in ovarioles for *P. grossa* and *P. thisbe* was 11.3 and 8.4, respectively (Table 1), with a range of 6–14 and 3–12. Because wasps require a host for each egg, and number of previous encounters with a spider was unknown, the number of eggs produced by each species of wasp prior to any hunting experience could not be determined from field data. However, I have reared both species of wasps from larvae feeding on *A. steindachneri* females (mean weight: 9.89 ± 0.61 g) in the laboratory and found that non-mated *P. grossa* (10–12 days of age) produced 9–21 eggs/female (mean: 16.2 + 3.2 g SE, n = 78) as compared to 4–14 (mean: 10.2 + 2.2, n = 38) for *P. thisbe* ($t = 7.09$, $P < 0.05$) (Punzo, unpubl. data).

For all observed encounters between *P. grossa* or *P. thisbe* and a host spider, wasps entered an occupied burrow by cutting through the silk covering over the burrow entrance and then forced the host to the surface. Attack and paralysis never occurred within the burrow. A wasp would typically approach the entrance of a spider burrow and tap its antennae along the edge of the opening. The time allocated by these wasps for each behavioral component of hunting behavior is shown in Table 2.

Pepsis thisbe females required significantly more time to complete the overall hunting sequence as compared to *P. grossa* ($F = 19.27$, $P < 0.05$) (Table 2). No significant interspecific differences were found for eviction behavior (EVB; Scheffe F, $P > 0.50$) or moving away and grooming (MG1, MG2, $P > 0.60$). Interspecific differ-

Table 2. Time (in min) allocated by females of *Pepsis grossa* (n = 54) and *P. thisbe* (n = 42) for various behavioral components of the overall hunting sequence during encounters with a host spider, *Aphonopelma steindachneri*. Data are expressed as means; numbers in parentheses represent ±SE. Values in rows followed by a different letter are statistically significant ($P < 0.05$). BA (burrow antennation); EVB (eviction behavior); AA (approach and antennation); MG1, MG2 (moving away and grooming); AP (antennation and paralysis); LB (lapping behavior); BO (burial and oviposition); BC (burrow closure).

Behavioral component	*Pepsis grossa*	*Pepsis thisbe*
BA	4.8a (0.8)	7.6b (1.1)
EVB	3.4a (0.3)	3.9a (0.4)
AA	8.3a (1.7)	5.1b (0.8)
MG1	4.6a (0.4)	5.2a (0.3)
AP	1.8a (0.2)	2.3a (0.5)
MG2	3.2a (0.6)	2.9a (0.3)
LB[1]	3.6a (1.1)	5.1b (1.8)
BO[2]	14.4a (3.5)	23.2b (4.6)
BC	57.3a (7.1)	73.8b (6.9)
Total:	101.4a	129.1b

[1] Lapping behavior occurred in 18 of 54 encounters for *P. grossa* (33.3%), and in 11 of 42 encounters for *P. thisbe* (26.2%).
[2] Represents data for situations in which a spider was buried in its own burrow.

ences for all other behavioral components were significant. As compared to *P. grossa*, *P. thisbe* females allocated significantly more time for burrow antennation (BA; Scheffe $F = 6.2$, $P < 0.05$), drinking behavior (DB; $F = 4.9$, $P < 0.05$), burial and oviposition (BO; $F = 7.1$, $P < 0.05$), and burrow closure (BC; $F = 6.9$, $P < 0.05$), and significantly less time for approach and antennation (AA; $F = 5.5$, $P < 0.05$).

Wasps of both species approached spiders that they had forced out of their burrows and then tapped the spider's body surface with their antennae. Antennae of *P. grossa* and *P. thisbe* initially made contact with the tarsus of one of the spider's forelegs in 50 of 54 (92.5%) and 39 of 42 (92.8%) encounters, respectively. In other cases, the antennae initially made contact with one of the spider'spalps. Subsequently, wasps of both species used their antennae to explore the lateral region of a spider's cephalothorax and abdomen. During antennation by *P. grossa*, 34 of 54 spiders (63%) exhibited no bodily movements as compared to similar values observed for *P. thisbe* (28 of 42, 67%, $P > 0.60$). For encounters with *P. grossa*, other spiders either remained stationary but exhibited slight movements of their foreleg (n = 2, 4%) or an elevation of the palps (n = 6, 11%), while the remainder (n = 12, 22%) exhibited a threat posture. Comparable values for similar responses of spiders to *P. thisbe* were 5% (n = 2), 9% (n = 4), and 19% (n = 8), respectively. In no case did a spider attempt to flee back into its burrow or attack the wasp, and wasps 'won' all observed encounters.

When initiating attack, wasps of both species showed a preference for grasping leg 3 or 4 of the spider (Table 3). Eight-one and 57% of *P. grossa* and *P. thisbe*, respectively, exhibited a rapid dash under the ventral region of the spider and used their mandibles to grasp leg 3 or 4 before attempting to insert their sting. Leg 1 was never grasped, and leg 2 in only 2.4–7.4% of encounters.

Sting insertion sites for *P.grossa* and *P. thisbe* are shown in Fig. 1. Examination of spiders post-paralysis showed that 78% of *P. grossa* females inserted their sting into the intersegmental membrane between the sternum and coxa 2 of the spider, and 22% between the sternum and pedipalp. In comparison, 88 and 12% of *P. thisbe* females, respectively, inserted their sting into the membrane between the sternum and coxa 1 or at the junction between the abdomen and cephalothorax. Mean time that elapsed between insertion of sting and immobilization (paralysis) of spider (indicated by curling of the legs under the spider's body) was 6.2 s ± 0.4 SE (range: 4–8 s) for *P. grossa* and 12.8 s ± 1.1 SE (range: 8–16 s) for *P. thisbe*. Regardless of insertion site, there was no significant difference in time required for paralysis for either species of wasp.

Table 3. Leg of spider (*Aphonopelma steindachneri*) grasped by females of *Pepsis grossa* and *Pepsis thisbe* when initiating attack. Data derived from a single observation of each wasp/spider encounter for 54 and 42 encounters, respectively, between *P. grossa* and *P. thisbe*, and a host spider. Spider legs on right and left side of the body (based on position of spider when a wasp was facing it) are designated as R and L, respectively, and legs are numbered 1 (forelegs) through 4 (hindlegs). Values in parentheses represent frequency of occurrence (%).

Spider leg grasped	*Pepsis grossa* (n = 54)	*Pepsis thisbe* (n = 42)
R1	0	0
L1	0	0
R2	4 (7.4)	1 (2.4)
L2	0	1 (2.4)
R3	20 (37)	14 (33.3)
L3	24 (44.4)	10 (23.8)
R4	4 (7.4)	7 (16.6)
L4	2 (3.7)	9 (21.4)

Only 33.3 and 26.2% of *P. grossa* and *P. thisbe* females, respectively, exhibited drinking behavior (DB, Table 2). Eleven of 18 (61%) females of *P. grossa* were observed to drink fluid oozing from the wound site (sting insertion site), while 7 (39%) wasps drank fluids from the spider's mouth cavity. For *P.thisbe*, the percentage of females that engaged in DB was 8 of 11 (73%) and 3 of 11 (27%) for the wound site and mouth cavity, respectively.

DISCUSSION

Physical dimensions and number of eggs for *P. grossa* and *P. thisbe* were similar to values reported for other species of *Pepsis* wasps of similar size. For example, eggs of *P. cerberus* Lucas and *P. mexicana* Lucas from another area of BBNP ranged from 4.19–4.29 and 4.25 vs. 4.31 mm (length), 1.26–1.38 and 1.18–1.29 mm (width), and 7.18–7.32 and 7.06–7.17 g (weight), respectively (Punzo 2005c). In like manner, number of eggs produced per female for *P. grossa* and *P.thisbe* were similar to values reported for other *Pepsis* wasps which range from 2–44/female (Haupt 1952, Evans and West-Eberhard 1970, Punzo 2000, 2005c). It has been shown that the number of eggs produced by *Pepsis* females (Evans 1953, Punzo 2005c), as well as in many other insects (Price 1975, Ito 1980, Nation 2002) is positively correlated with body size.

Although a majority of paralyzed spiders found with an attached *Pepsis* egg (where encounters with a wasp had not been observed) contained female spiders (68%), almost 1/3 contained a male. Thus, it appears that *Pepsis* wasps are opportunistic hunters and will readily attack a male tarantula even though males are usually smaller than females. This is in general agreement with previous laboratory or field observations showing that *Pepsis* wasps will attack, paralyze, and deposit an egg on male and female theraphosid hosts (Kurczewski and Kurczewski 1968, Punzo 2000). An experimental protocol that might allow us to determine whether female *Pepsis* wasps have any 'preference' for spiders of different sexes would be to observe the response of mated female wasps when given a choice between a male and female spider. If naïve females are used (no previous encounter with a spider), one can also assess whether such a preference, if exhibited, had an innate component.

Little information is available on the number of eggs produced per female for *Pepsis* wasps. A previous study yielded some data for pepsine wasps collected from Persimmon Gap, a site 48 km to the northeast of TF that also lies within BBNP (Punzo 2005c). Number of eggs in ovarioles from wasps collected immediately after mating (before they started to hunt for hosts) ranged from 5–26 (mean: 12.7 ± 2.8 SE) and 4–20 (mean: 11.8 ± 1.7) eggs per female, for *P. cerberus* and *P. mexicana*, respectively. It is difficult to extrapolate and compare these data with values reported for *P. grossa* (11.3) and *P. thisbe* (8.4) in the present study because there was no way of knowing how many prior encounters these wasps had with a host before they were collected. These compare

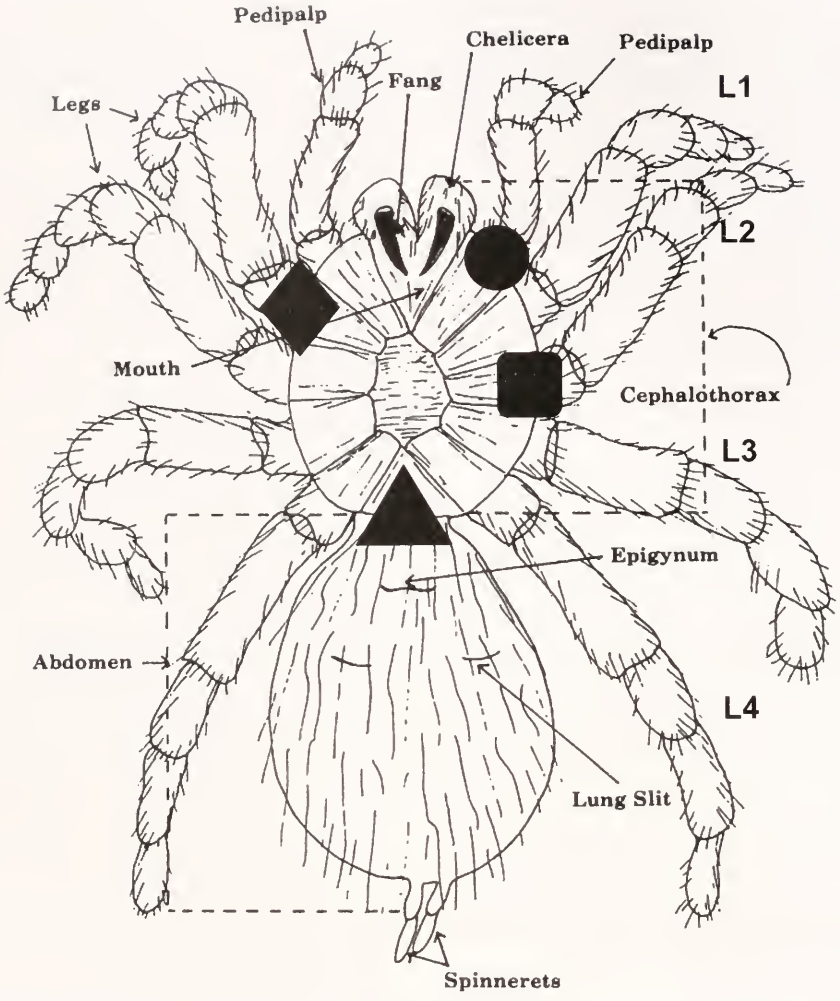

Fig. 1. Ventral body region of *Aphonopelma steindachneri* showing insertion sites (wound sites) for the sting of *Pepsis grossa* and *P. thisbe*. Solid circle and square (intersegmental membrane between sternum and pedipalp, and sternum and coxa 2, respectively) are insertion sites for *P. grossa*: solid triangle and diamond (membrane between sternum and coxa 1, and at junction of cephalothorax and abdomen, respectively) are insertion sites for *P. thisbe*. Legs: L1–L4.

to 9–21 eggs for *P. grossa* and 4–14 for *P. thisbe* reared in the laboratory (Punzo, unpubl. data).

Spiders paralyzed by *P. grossa* and *P. thisbe* varied in body weight. Previous research has demonstrated that adult size (as assessed by head capsule width, length of legs or wings) attained by other species of spider wasps is positively correlated with the mass attained by their last-instar larvae (Vinson 1984, Punzo 2005c), which in turn is positively correlated with the mass of the spider that the larvae fed on (Price 1997, Punzo 2005c). This most likely accounts for the ranges in adult size observed in male and female *Pepsis* wasps in the field. Although empirical evidence is lacking, it would be interesting to determine to what extent (if any) a decision made by a female *Pepsis* wasp concerning size of host suitable for attack may be influenced by the wasp's size.

There are relatively few detailed observations and analyses on foraging (Cazier

and Mortenson 1964, Punzo and Ludwig 2005, Punzo 2006a,b), territoriality (Rau and Rau 1918, Punzo 2000), dispersal (Evans and West-Eberhard 1970), diel periodicity (Punzo 2005c), and hunting behavior (Petrunkevitch 1952, Williams 1956, Punzo 2005a) in *Pepsis* wasps under natural conditions. Although many aspects of overall hunting behavior for wasps of this genus are similar across species, the results of this field study indicate that there is some interspecific variation associated with certain behavioral components of hunting between *P. grossa* and *P. thisbe* which include frequency of drinking behavior and sting insertion sites. At the Tornillo Flat (TF) study site, females of both species approached a burrow occupied by adult females of *A. steindachneri* and tapped their antennae along the edges of the opening (burrow antennation, BA). Wasps then entered the burrow after cutting through the silk covering and forced the spider out onto the ground surface (eviction behavior, EVB). These behaviors have been reported for encounters between theraphosid spiders and other species of *Pepsis* wasps (Buckley 1862, Petrunkevitch 1926, 1952, Passmore 1936, Punzo 2005a), as well as *P. grossa* (as *formosa*) (Punzo and Garman 1989, Punzo 1991) and *P. thisbe* (Punzo 1994b), that were staged in the laboratory.

Because *A. steindachneri* is the only species of theraphosid spider known to occur at TF, all females of *P. grossa* and *P. thisbe* utilized this species as a host for their larvae. At sites 25–80 km to the north, these two species of wasps, along with *P. mildei* Stål, are known to utilize both sexes of two other theraphosids, *Aphonopelma* (as *Rhechostica*) *hentzi* and *Dugesiella* (as *Aphonopelma*) *echina* Hentzi as a host (Punzo and Garman 1989, Punzo 1991). In southern Texas (Hidalgo County), *P. grossa* (as *formosa*) utilizes both sexes of the theraphosids *A. harlingenum* (Chamberlin) and *A. heterops* (Chamberlin) as hosts, although it shows a strong preference for *A. harlingenum* (Punzo 2006b). Farther to the west, in Arizona and California, *P. grossa* is known to hunt another theraphosid, *A. chalcodes* (Chamberlin) (Cazier and Mortenson 1964). In southern California, *P. thisbe* hunts two theraphosid species, *A. reversum* Simon and *Eurypelma* (as *Aphonopelma*) *eutylenum* (Ausserer) (Williams 1956). From the same region, *P. mildei* has been reported to utilize females of the trapdoor spider *Bothriocyrtum californicum* (Chamberlin and Ivie) (Passmore 1933), a mygalomorph spider from an entirely different family (Ctenizidae). However, I have never found a nest containing any species of paralyzed trapdoor spider with a *Pepsis* larvae, or egg at any of a number of locations in BBNP or Big Bend Ranch State Park (Presidio Co., Texas) (Punzo unpubl. data).

These various host records suggest that *Pepsis* wasps have the ability to utilize immatures and adult males and females of a variety of theraphosid spiders as hosts, depending on the theraphosids available at any particular site. Presumably, during the course of evolution in pompilid wasps, selection favored a preference for hunting a single, larger host for each wasp larva. Many species of spider wasps in this genus are among the largest wasps in the New World (Hurd 1952, Vardy 2000, 2002) and adults develop from larvae that attain lengths in excess of 27 mm and can weigh over 5 g (Punzo 2000). In order for a female to provide an adequate amount of food for such large larvae, each larvae would have to be provided with a high number of smaller hosts either together or over a continuous period of time (*progressive provisioning*) as opposed to providing all required food at one time (a single large host or mutliple small ones, e.g. by *Trypoxylon* wasps) at one time (*mass provisioning*) (O'Neill 2001). There are obvious trade-offs that are involved. Progressive provisioning involving several smaller prey would require more energy and increase exposure of wasps to potential

predators, while requiring more handling time but less risk from the prey. In contrast, a single, larger, more formidable host, may require less handling time but pose a higher risk from the prey, whilst requiring less overall energy expenditure and a decreased probability of encountering a predator.

The data collected to do not point to specific niche divisions between *P. grossa* and *P. thisbe* at the TF site. I did not observe any significant interspecific differences in the sex or size of spiders selected, nor in temporal patterns of hunting activity. Adult wasps of both species begin to emerge from their nests during late March and continue to do so until August. Females of both species were observed hunting during daylight and evening hours. At sites further south (Zapata Co., Texas), *P. thisbe* begins to emerge in mid-March, whereas *P. grossa* adults are not seen until mid-April (F. Punzo unpubl. data). Perhaps host spiders occurred at sufficiently high densities during the course of the present study at the TF site so that any need for resource paritioning was reduced.

Future studies should further analyze host preference in *Pepsis* wasps. For example, at locations where a *Pepsis* wasp is known to utilize more than one theraphosid species, it would be instructive to assess any differences that may occur with respect to duration of embryonic development, larval growth rate and number of larval instars, size of emerging adults, adult longevity, fecundity, flight endurance, and host preference, for wasps developing on different hosts.

Overall hunting behavior of *Pepsis* wasps (*P. grossa*, *P. thisbe*, *P. mildei*, *P. marginata*, and *Pompilus* spp). can be categorized into several distinct behavioral components (Table 2), one of which may or may not occur (DB) (Petrunkevitch 1926, Passmore 1936, Evans 1953). These behavioral components were traditionally interpreted as examples of genetically-determined, inflexible acts referred to a fixed action patterns, FAPs, which are characteristic of instinctive (innate) behavior (Tinbergen 1951). More recent studies, based on sequential laboratory-staged contests between *Pepsis* wasps and spiders, have shown that the amount of time required to perform some behavioral acts decreases as a function of increasing number of encounters (experience) (Punzo and Garman 1989, Punzo, 1991, 2005a).

The term 'modal action pattern' (MAP) has been used to describe components of innate behavior that exhibit some degree of plasticity (Barlow 1977). The acts that have been shown to improve with experience include initial approach and antennation (AA) and attack and paralysis (AP) (Table 2), while the time required for other behavioral components does not. This suggests that some degree of learning is associated with hunting behavior in these wasps (Punzo 1996). It is interesting to note that those acts which a wasp can perform more quickly with experience are precisely those which present the most risk for a wasp. AA requires that a wasp approach within a close distance of the spider and actually touch the spider's body with its antennae, placing it well within the strike distance of the spider (Punzo 2007b). AP requires the wasp to move directly under a spider's body, often passing directly below its fangs, grasp a leg, and insert its sting. In contrast, performance of behavioral acts that pose no risk because the spider has already been immobilized (MG2), or are most likely subject to biomechanical constraints (BO, and BC), do not 'improve' with experience (Punzo 1991, 1994b). Similarly, MG1, which increases the distance between protagonists and thereby decreases risk for a wasp, is not performed more rapidly with increasing number of encounters (Punzo and Garman 1989, Punzo 2000).

During attack, these wasps showed a marked preference for grasping legs 3 or 4 of a spider before stinging it. Perhaps the positions of legs 3 and 4, relative to the

center of gravity for a spider, make it easier for a wasp to obtain the leverage required to insert its sting through an appropriate site on the spider's ventral surface in the least amount of time. The faster a wasp insert its sting the more rapidly it can immobilize a formidable host and reduce the probability of retaliation by the spider. Experiments where a wasp is presented with a spider whose legs 3 or 4 have been removed, would force a wasp to grasp leg 1 or 2, or refuse to attack at all, and would provide a way to assess any possible biomechanical advantage associated with grasping various legs.

All observations of encounters between *Pepsis* wasps and theraphosids have shown that a wasp's sting is directed into the ventral body region of a spider (Punzo 2007b, and references cited therein). Females of *P. grossa* and *P. thisbe* showed a marked preference when choosing a site on the spider's body in which to insert their sting. Little information is available for sting insertion sites for *Pepsis* wasps. Petrunkevitch (1926) observed a female of *P. marginata* insert her sting between the third and fourth right coxae when attacking the theraphosid, *Cyrtopholis portoricae* Simon. Another wasp inserted its sting into the intersegmental membrane between the sternum, maxilla and coxa 1. In an encounter with the theraphosid *Dugesiella hentzi*, a *Pepsis* wasp of undetermined species inserted its sting through the membrane between coxa 3 and coxa 4 (Baerg 1958).

The site preferred by females of *P. grossa* and *P. thisbe* was the intersegmental membrane between coxa 2 and sternum, and between coxa 1 and sternum, respectively. These, as well as the other sting insertion sites observed in this study (membrane between pedipalp and sternum, *P. grossa*; junction between abdomen and cephalothorax, *P. thisbe*), all allow a wasp to deliver its venom into the prosomal nerve mass which supplies motoneurons to muscles involved in movments of all legs, chelicerae, and fangs (Foelix 1996, Punzo 2007b). Some investigators have observed instances in which a wasp failed to locate an insertion site during its first attack on a spider, moved a short distance away, and then attacked again, successfully paralyzing its host (Petrunkevitch 1952, Williams 1956, Baerg 1958). Nonetheless, once the sting delivers venom into the prosomal nerve mass, paralysis of the spider occurs very rapidly as indicated by a curling of the spider's legs under its body, slight twitching movements of some appendages, and then complete immobilization (Petrunkevitch 1926, Cazier and Mortenson 1964, Punzo 2000).

These results on sting insertion sites also indicate that there is behavioral variation exhibited by these wasps. This suggests several interesting questions that future studies should address: do individual wasps choose the same insertion site for all encounters, or do they vary? If sting insertion sites are 'fixed' for individual females this would suggest that the behavioral program has a genetic basis (innate). If so, breeding experiments involving males with females showing different behavioral phenotypes might shed some light on the patterns of inheritance involved in this behavior. Secondly, is there a relationship between a particular insertion site and time required to immobilize a spider?

Nutritional state (body condition) may afford a possible explanation for why drinking behavior (DB) occurs in only some encounters. Drinking hemolymph oozing from a host's wound site may provide necessary nutrients to meet the energetic demands of flight which wasps engage in when searching for hosts, as well as those of venom production, handling time, and burrow closure. Drinking fluids from a spider's mouth cavity may help wasps to maintain proper water balance of body fluids. Similar behavior has been reported for species in other wasp families. For example, Tinbergen (1972) observed that females of the digger wasp, *Philanthus*

triangulum Fabricius, which selectively hunt honeybees, *Apis mellifera* L., press the abdomen of a paralyzed bee through their mandibles and lick up the fluid (nectar) extruded from the bee's mouth. Species of spider wasps from other genera are also known to drink fluids from a host's mouth cavity or wound site (Petrunkevitch 1952, Evans 1953, Williams 1956, Evans and West-Eberhard 1970, Punzo 2000).

It may be that wasps engage in DB only after a certain number of foraging bouts have occurred resulting in a need to replenish nutrients and/or body fluids. Experimental protocols using a tethered flight apparatus should be used in future studies to test this hypothesis. Different female wasps could be subjected to forced flight tests for varying periods of time and then allowed to encounter a host. If the hypothesis is true, wasps that are subjected to longer bouts of flight (and thus expend more energy, and lose more water by evaporation) should be more likely to engage in DB than wasps subjected to flying for shorter periods of time. Such an experimental design would also allow one to determine the amount of flight time required to initiate LB in a particular wasp species.

The confines of a spider's burrow might not provide enough room for a wasp to maneuver in such a way as to effectively administer a sting to its host. This may account for the fact that all wasps observed at the TF site forced a spider out of its burrow and onto the ground surface (eviction behavior, EVB) before attacking their host. Similar EVB has been observed for *Pepsis* wasps presented with tarantulas that have been allowed to excavate burrows within their cages under laboratory conditions (Petrunkevitch 1926, Punzo and Garman 1989, Punzo 1991, 1994b).

Interspecific differences in the amount of time required to complete the overall hunting sequence among *P.grossa* and *P. thisbe* in the field may be associated with some wasps of either species having had more encounters with hosts than other wasps. It may also reflect genetically-based differences in synaptic events associated with afferent (sensory) neural pathways involved with detection and identification of hosts and/or efferent (motor pathways) involved in the control of bodily movements required for various behavioral acts.

On a final note, theraphosid spiders are typically aggressive and innately strike at arthropods that wander within their prey awareness area (Punzo 2007b). The fact that no spider attempted to seize a wasp suggests that the spider's attack response is somehow inhibited. It has been suggested that these wasps may release some chemical compound(s) or possess chemosensory cues associated with their epicuticle that inhibit spider's from attacking them (Petrunkevitch 1952, Punzo 2000). Petrunkevitch (1926) observed that *P. marginata* from Puerto Rico produced a "pungent odor" when initially making contact with a theraphosid host and argued that the substance responsible for this odor might somehow diminish the aggressiveness of the spider. Others have pointed out that the smooth surface of a wasp's cuticle, combined with its high degree of hardness, makes it difficult for a spider's fangs to penetrate a wasp's integument (Petrunkevitch 1926, Passmore 1936).

It should be pointed out that Petrunkevitch (1926) observed a theraphosid (*Cyrtopholis portoricae* Simon) that unsuccessfully attempted to grasp a female of *P. marginata* Lucas with her fangs as the wasp passed under the spider. Cazier and Mortenson (1964) observed a *Pepsis grossa* (as *formosa*) female entering a burrow occupied by *Aphonopelma* sp., and after a few minutes the spider emerged from its burrow with its anterior two legs wrapped around the wasp and its chelicerae inserted into the wasp's abdomen. Nonetheless, the wasp was able to sting the spider. After being stung, the spider released the wasp which exhibited erratic movements and was un-

able to fly. The spider's right leg was rigidly extended forward, making locomotion awkward. After several minutes, the wasp and spider were placed in a screened plastic container and initially both animals avoided one another. When observed 45 min later, the spider was engaged in eating the wasp. These observations suggest that: (1) cues potentially responsible for inhibiting a spider's strike response may not always be effective (2) varying degrees of effectiveness may be species-specific; or (3) mutations may account for differences in the chemical profile of the wasp's cuticle and certain profiles may be less effective at deterring a spider's strike than others.

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Systematic Studies on the Pompilidae Occurring in Japan: Genus *Irenangelus* Schulz (Hymenoptera: Pompilidae: Ceropalinae)

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Abstract.—The Japanese species of the genus *Irenangelus* Schulz (Pompilidae: Ceropalinae) are revised. Three new species are described: ***I. hikosanus* Wahis**, ***I. nambui* Shimizu**, and ***I. punctipleuris* Wahis**. *Irenangelus hikosanus* occurs in Japan (Honshu, Shikoku, Kyushu), Korea, Taiwan, and China; *I. nambui* occurs in Japan (Honshu) and Korea; *I. punctipleuris* is broadly distributed from Japan through the Philippines and Malaysia to India and Sri Lanka.

Irenangelus Schulz 1906, like *Ceropales* Latreille 1796, is one of the most aberrant genera of the family Pompilidae. All members of both genera have an uncoiled antenna, reniform eyes with the inner orbits strongly emarginate and diverging above, a fully exserted labrum in both sexes, and a strongly compressed metasomal sternum VI produced beyond tergum VI in the female.

Evans (1969, 1987) reviewed the Neotropical species of *Irenangelus*. In these papers he treated ten species, seven of which were new, and regarded *Xanthampulex* Schulz 1906 as a synonym of *Irenangelus*. Kimsey and Wasbauer (2004) revised the New World species of *Irenangelus*, adding two new species. As regards the Old World species of *Irenangelus*, Cameron (1891, 1896), Bingham (1896), Schulz (1906), Turner (1910), Rohwer (1919), Banks (1934), and Wahis (1988) described either single species or, at most, a few new species, but no comprehensive revisionary studies have been published.

Species of *Irenangelus* have long been recognized as cleptoparasites of other pompilids, as are species of *Ceropales*. Thus, Williams (1919) reared an *Irenangelus* wasp from a nest of *Auplopus nyemitawa* (Rohwer 1919) and several wasps in this genus from cocoons of nests of *Tachypompilus analis* (Fabricius 1781) in the Philippines. At least one wasp reared belonged to *I. luzonensis* (Rohwer 1919). In Costa Rica, Wcislo *et al.* (1988) observed females of *I. eberhardi* Evans 1987 fly or perch near nests of *Auplopus semialatus* Dreisbach 1963, enter an open cell containing a spider, and extend her gaster deep into the cell. They reared several wasps of this parasite from one of the nests of *A. semialatus*. Shimizu (see below) found females of a Japanese species of *Irenangelus* attempting to oviposit eggs into a slit of the booklung of heteropodid spiders that the host pompilids had captured and then transported.

Irenangelus is mainly distributed in the Oriental and Neotropical regions. In Japan only one species of the genus has been known since Yasumatsu (1933) recorded the species from Honshu, Kyushu, and Taiwan as *Xanthampulex pernix* (Bingham 1896). This species is distributed also in Korea and China, and differs from *X. pernix*, which was originally recorded from

"Tenasserim" (Burma). Recently specimens of a further two species of this genus were collected from Honshu, Japan. One of them is found in Korea in addition to Japan, and the other occurs from Japan through Southeast Asia to South Asia. It was found that these three species are undescribed.

In this paper, we review the generic characters and phylogenetic relationships of *Irenangelus*, describe three new species and provide a key to their identification.

MATERIALS AND METHODS

The terminology of the wing veins and cells follows Day (1988). The following morphological terms and abbreviations are used: antennocular line, the anterior margin of the frons in dorsal view; scutal groove, a pair of longitudinal grooves between the notaulus and parapsidal sulcus on the mesoscutum (Evans (1969) and Kimsey and Wasbauer (2004) called this the "notaulus"); LID, the lower interocular distance; MID, the middle interocular distance; OOL, the ocello-ocular line; POL, the postocellar line; SMC, the submarginal cell of the fore wing; UID, the upper interocular distance.

Measurements were made in the following ways: clypeus length versus breadth, being measured comparing the length of the clypeus from the uppermost point of the front-clypeal sulcus to the apical margin to the maximum breadth of the clypeus; labrum length versus breadth, being measured comparing the longest part of the labrum to the breadth across the base of the labrum; breadth of flagellomere I, being measured across the maximum breadth of flagellomere I in dorsal view. In the description of each species, the measurements of the holotype are given in parentheses.

Specimen depositories are abbreviated as follows: ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark; UCDC, R. M. Bohart Museum of Entomology, University of California, Davis, California, USA; ELKU, Collection of Entomological Laboratory, Kyushu University, Fukuoka, Japan; AEIC, American Entomological Institute, Gainesville, Florida, USA; FSAG, Entomologie fonctionnelle et évolutive, Faculté universitaire des Sciences agronomiques, Gembloux, Belgique; RMNH, Nationaal Naturhistorische Museum, Leiden, Netherlands; BMNH, Natural History Museum, London, UK; OMNH, Osaka Museum of Natural History, Osaka, Japan; CNC, Canadian National Collection of Insects, Ottawa, Ontario, Canada; NSMT, Department of Zoology, National Science Museum, Tokyo, Japan; TMUB, Laboratory of Zoological Systematics, Department of Biological Sciences, Tokyo Metropolitan University, Tokyo, Japan; USNM, National Museum of Natural History, Washington, D. C., USA.

SYSTEMATICS

Genus *Irenangelus* Schulz

Irenangelus Schulz 1906: 175. Type of genus: *Irenangelus hornus* Schulz 1906: 160, by monotypy.

Xanthampulex Schulz 1906: 183. Type of genus: *Xanthampulex trifur* Schulz 1906: 183, by monotypy.

Description.—Further to the descriptions of this genus by Evans (1969) and Kimsey and Wasbauer (2004) we note the following characteristics: gena flattened or concave just posterior to outer orbit at least below; posterolateral margin of pronotum almost straight (Figs 2F, 3D); scutal groove deeply impressed in many species (Figs 1A, 2C); metapostnotum well developed at least medially (Figs 1A, D, 2A, F, 3D); fore wing vein M reaching outer wing margin (Figs 2A, 5A, B); metatibia with longitudinal sharp groove along upper margin of brush on inner side (Fig. 2A); apicoventral seta on metatarsomere V long and setiform (see Shimizu *et al.* 1998: fig. 3); female laterosterna of metasomal sternum VI extending dorsad, scarcely overlapping to envelope sting apparatus; sting almost

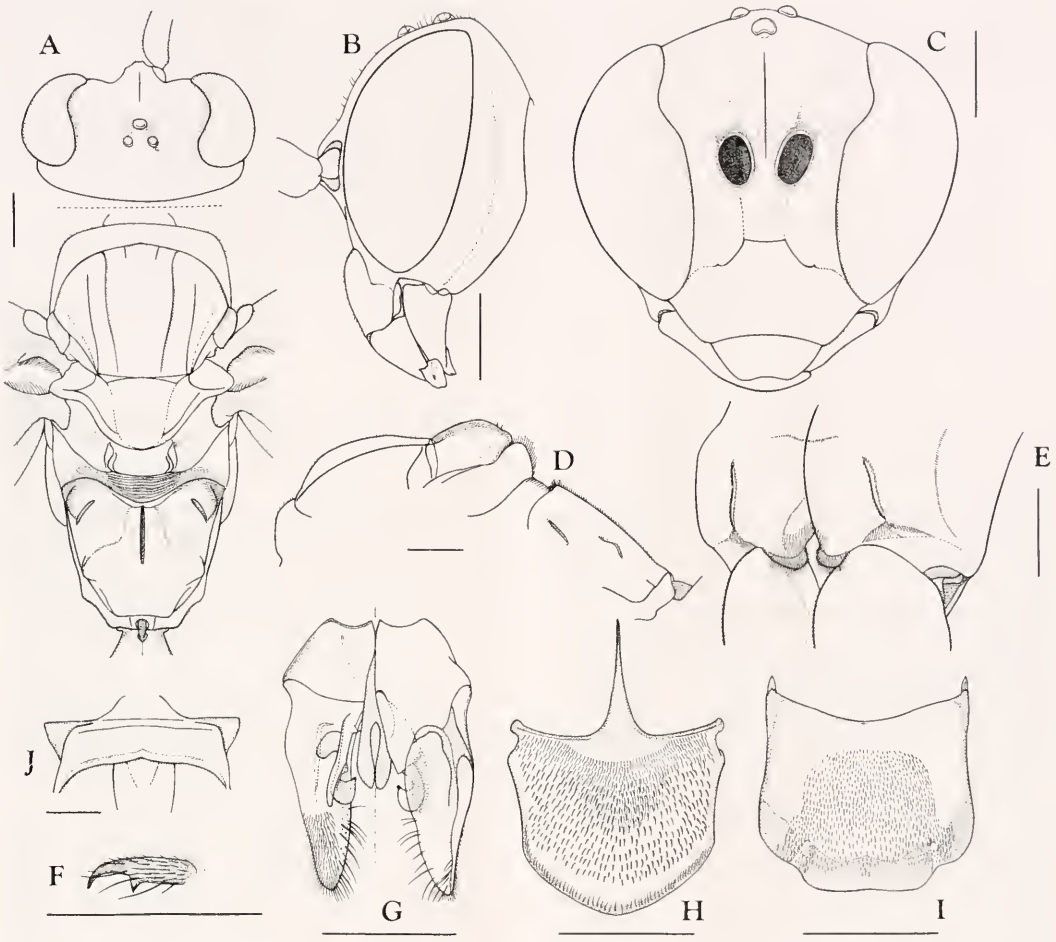

Fig. 1. *Irenangelus hikosanus* n. sp. (A–F, holotype female; G–I, paratype male from Japan) and female *I. pernix* Bingham from Bali, Indonesia (J). A, Head and mesosoma, dorsal view; B, head, lateral view; C, head, frontal view; D, mesosoma, lateral view; E, mesosternum and mesocoxa, ventrolateral view; F, right metatarsal claw, outer view; G, genitalia (left half, ventral view; right half, dorsal view); H, subgenital plate, ventral view; I, sternum VI, ventral view. Scale lines: 0.5 mm.

straight; male sternum VI without a pair of sublateral hook-like projections posteriorly (Fig. 1I); digitus volsellaris with large semicircular emargination on inner margin (Figs 1G, 2I, 3L).

Diagnosis.—*Irenangelus* is closely related to *Ceropales*, forming a monophyletic group, the subfamily Ceropalinae (Shimizu 1994, Pitts et al. 2006). These two genera are distinguishable on the characteristics shown in Table 1.

Phylogenetic relationships.—On the basis of morphological characteristics, both Shimizu (1994) and Pitts et al. (2006) treated the Ceropalinae (*Ceropales* + *Irenangelus*) as the most basal clade in the Pompilidae. This subfamily is thus considered to be the sister group to the rest of the family. Based on this hypothesis, there is a biological inconsistency: although the Ceropalinae are placed as the earliest offshoot of the pompilid stock, all species of the subfamily whose behaviour is known are cleptoparasitic. To avoid this contradiction, Shimizu (1994) considered that the behavioural type of the Ceropalinae has evolved directly from that of the parasitoids, which is the most likely life history of a common ancestor of the

Table 1. Comparison of differential characters between *Irenangelus* and *Ceropales* in the broad sense, including *Priesnerius* and *Hemiceropales*.

Irenangelus	*Ceropales*
1. Metacoxa normal-sized, less than 1.5× as long as mesocoxa.	Metacoxa much larger than mesocoxa, more than 1.5× as long as mesocoxa.
2. Ventral angle of pronotum short and blunt, not attaining dorsal margin of procoxa (Fig. 3D).	Ventral angle of pronotum long and acute, partly covering dorsal margin of procoxa.
3. Posterolateral margin of pronotum almost straight (Figs 2F, 3D).	Posterolateral margin of pronotum strongly curved inward.
4. Inner margin of male protarsomere V not produced.	Inner margin of male protarsomere V produced ventrally.
5*. Male subgenital plate flat or gently convex (Figs 1H, 2H, 3L).	Male subgenital plate tectate with median carina.

*Character treated by Kimsey and Wasbauer (2004).

Pompilidae. Similarly, Day (1988: 16) stated: "it seems more probable that *Ceropales* has evolved from an ancestral group already specialized as ectoparasitioids." This presumption seems likely given that the two important characteristics of Ceropalinae females are shared with other pompilids known to behave as parasitoids, viz- (i) the strongly exposed clypeus, and (ii) the laterally compressed sternum VI.

Biology.—One or more Philippine species of *Irenangelus* are known to be cleptoparasites of *Auplopus uyemitawa* (Pepsinae) and *Tachypompilus analis* (Pompilinae), and *I. eberhardi* a cleptoparasite of *Auplopus semialatus* (Pepsinae) (Williams 1919). Shimizu observed the cleptoparasitic behaviour of *I. hikosanus* Wahis n. sp., which pursues its host pompilid *Platydialepis ryoheii* (Ishikawa 1956) (Pepsinae) as the latter transports her prey, *Heteropoda forcipata* (Karsch 1881) (Heteropodidae) to her nest. Eventually the parasite pounces on the spider and extends her gaster, attempting to insert its tip into a slit of the spider's booklung. The details of this behaviour will be treated in a separate paper.

Distribution.—This genus is known from Oriental, Neotropical, Australian, East Asian, and Madagascan Regions (see Wahis 1988), but is best represented in the first two regions.

KEY TO FEMALES AND MALES OF *IRENANGELUS* OCCURRING IN JAPAN

1. Flagellum crenulate in profile, *i.e.*, flagellomeres II–X each with angular swelling below (Fig. 3A); all tarsal claws bifid, inner ray truncate (Fig. 3G); propodeum transversely striate; metasomal tergum I gradually narrowed and petiolate (tergum I narrower immediately behind articulation with propodeum than width at articulation itself) (Fig. 3E) or parallel-sided basally; head and mesosoma with irregularly-distributed punctures (Figs 4C–F). (Head and mesosoma black, variegated with bright yellow markings; metasoma and legs predominantly reddish brown; body length 8–12 mm) . . . . . ***I. punctipleuris* Wahis, n. sp.**

– Flagellum not crenulate in profile; all tarsal claws dentate (Fig. 1F) or sub-bifid (Fig. 2G), inner ray acute; propodeum smooth, never striate; metasomal tergum I abruptly narrowed, not petiolate or parallel-sided basally (Fig. 2A); head and mesosoma impunctate (Fig. 4B) 2

2. Propodeum with lateral tubercle between spiracle and posterior rim (Fig. 1A); interantennal area distinctly raised (Figs 1B, 4B); fore wing crossvein cu-a originating at or slightly distal to separation of vein M+Cu (Fig. 5A); fore wing

SMC3 removed by approximately its own length from outer wing margin; apical margin of subgenital plate strongly convex (Fig. 1H); body predominantly yellowish brown; body length 8–15 mm ..... ***I. hikosanus* Wahis, n. sp.**

– Propodeum without lateral tubercle between spiracle and posterior rim (Fig. 2A); interantennal area not raised, continuous to upper frons (Fig. 2D); fore wing crossvein cu-a originating slightly basad of separation of vein M+Cu (Fig. 2A); fore wing SMC3 removed by much more than its own length from outer wing margin; apical margin of subgenital plate slightly emarginate or almost truncate (Fig. 2H); body predominantly blackish brown to black; body length 5–9 mm .... ***I. nambui* Shimizu, n. sp.**

Irenangelus hikosanus Wahis, new species
(Figs 1A–I, 4B, 5A)

Xanthampulex pernix: Yasumatsu 1933: 143, figure 1, ♂♀, misidentification; Kim 1970: 807.
Irenangelus pernix: Lelej et al. 1994: 145; Lelej et al. 1995: 46; Shimizu 1994: 45; Shimizu 1996: 507; Shimizu et al. 1998: 429, figure 3.

Female.—Length: Body 9.1–14.5 (9.8) mm; fore wing 8.7–11.3 (8.7) mm. *Coloration*: Body and appendages predominantly yellowish brown and polished. Following light yellow: mandible (apical portion dark brown), clypeus (lateral side sometimes yellowish brown), frons along inner orbit, gena along outer orbit, ventral margin of scape, maxillary and labial palpi, pronotum posteriorly and laterally, discs of scutellum and metanotum, posterior rim of propodeum, procoxa, and sometimes interantennal tubercle ventrally, labrum, and episternum posteriorly. Apical 4 or 5 flagellomeres black dorsally. Basilateral and posterior portions of metasomal tergum I and posterior portions of following terga more or less darkened. Metatarsus becoming darker towards apex. Wings hyaline with yellowish brown tint, iridescent in certain lights, narrowly and weakly infuscate along outer margins. Pterostigma dark brown. *Punctation*: Body devoid of punctures. *Pubescence and setae*: Pubescence on body usually very short and decumbent; metanotum, lateral portion of metapostnotum, and propodeum with long, sub-erect, brown pubescence. Vertex, labrum, mandible, propleuron, and sterna V-VI with short yellowish brown to brown setae; remainder of body and legs almost devoid of setae. *Head*: 1.1–1.2 (1.1)× as broad as long. Vertex moderately to strongly convex between eye tops (Fig. 1C). Frons distinctly tuberculate between antennal sockets (Figs 1B, 4B); upper frons broadly depressed along median line, the latter being sharply impressed on antennal tubercle but becoming obscure near anterior ocellus. Antennocular line depressed beside antennal tubercle (Fig. 1A). Inner orbits distinctly emarginate at upper 1/3, gently convergent below (Fig. 1C). UID:MID:LID=9.1–9.4:10:6.3–6.7 (9.4:10:6.3). MID 0.57–0.60 (0.58)× head width. Ocelli forming acute triangle, this area being distinctly raised. POL:OOL= 1:2.5–3.1 (3.1). Clypeus slightly convex, 1.8–2.0 (2.0)× as broad as long; anterior margin truncate, weakly and arcuately emarginate (Fig. 1C); lateral sides strongly convergent towards apex. Labrum 1.8–2.1 (2.1)× as broad as long; anterior margin feebly and triangularly emarginate. Mandible narrowly rounded without sharp carina laterally. Malar space short (Fig. 1B). Genae 0.4–0.5 (0.5)× eye width in profile, roundly receding in dorsal view. Scape with carina long but not sharp beneath; face slightly concave laterally in dorsal view. Flagellomere I 2.1–2.9 (2.5)× as long as wide and 0.34–0.48 (0.44)× as long as UID; flagellomeres I and II in ratio of 10:9.3–11 (10:10). *Mesosoma*: Pronotum

short (Fig. 1A); anterior margin of disc arcuately convex in dorsal view, its anterolateral corner rounded; lower anterolateral tubercle not much swollen, being almost concealed by disc in dorsal view (compare Fig. 1A with Fig. 1J: *I. pernix*); posterior margin arcuate with small median notch. Mesoscutum with scutal groove sharply impressed anteriorly, becoming shallower and broader posteriorly, but almost attaining scuto-scutellar sulcus; parapsidal sulcus appearing as a fine, raised line; posterolateral margin broadly reflexed. Discs of scutellum and metanotum remarkably projecting, the latter steeply falling posteriorly (Fig. 1D). Posteromedian lobes of mesosternum well developed and digitate, apices close to each other (Fig. 1E). Metapostnotum 0.7–1 (0.7)× as long as metanotum at midline, deeply sunken between metanotum and propodeum (Fig. 1D), with fine, transverse striae. Propodeum strongly depressed along anterior margin, almost linearly sloping in profile, with one or two lateral tubercles between spiracle and posterior rim (Fig. 1A); infrastigmal tubercle roundly raised; median groove impressed only anteriorly; surface smooth, not striate. *Metasoma*: Slender and almost parallel-sided medially. Tergum I abruptly narrowed, not petiolate or parallel-sided basally. *Legs*: Longer spur of metatibia 0.69–0.77 (0.73)× as long as metatarsomere I. Tarsal claws with vertical tooth near middle (Fig. 1F). *Wings*: Fore and hind wing venation as shown in Fig. 5A. Fore wing crossvein 2r-rs originating beyond middle of pterostigma. Crossvein cu-a originating at or slightly distal to point of separation of vein M+CuA. SMC2 trapezoid, receiving crossvein 1m-cu at basal 0.54–0.70 (0.58). SMC3 narrowed on vein Rs by 0.70–0.82 (0.77)× its length on vein M, 1.1–1.4 (1.3)× as long as SMC2 on vein M, 1.2–1.5 (1.4)× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at basal 0.55–0.61 (0.55). Hind wing crossvein rs-m straight, oblique to vein M. Crossvein cu-a at angle of approximately 150° to vein A.

Male.—Very similar to female. *Length*: Body 7.1–12.4 mm; fore wing 7.1–11.4 mm. *Head*: 1.1–1.2× as broad as long. UID:MID:LID=9.0–9.3:10:6.5–6.8. MID 0.57–0.62× head width. POL:OOL=1:2.3–2.6. Clypeus 1.8–2.0× as broad as long. Labrum 1.8–1.9× as broad as long. Gena 0.4–0.5× eye width in profile. Flagellomere I 2.0–2.5× as long as wide, 0.34–0.43× as long as UID; flagellomeres I and II in ratio of 10:9.2–11. *Mesosoma*: Metapostnotum 0.8–1× length of metanotum at midline. *Legs*: Longer spur of metatibia 0.69–0.76× length of metatarsomere I. *Wings*: Fore wing SMC2 receiving crossvein 1m-cu at basal 0.56–0.70. SMC3 narrowed on vein Rs by 0.67–0.79× its length on vein M, 1.1–1.4× length of SMC2 on vein M, 1.1–1.4× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at basal 0.55–0.67. *Subgenital plate* (Fig. 1H): Lateral sides gently convergent towards apex; apical margin sub-triangularly convex; ventral surface covered with minute setae except for subapical portion. *Genitalia* (Fig. 1G): Paramere with strong setae apicomedially; parapenial lobe slightly extending beyond apex of aedeagus.

Distribution.—Japan (Honshu, Shikoku, and Kyushu), Korea, Taiwan (Yasumatsu 1933), and China (Fig. 6).

Type material.—Holotype ♀ (ELKU), Japan, Kyushu, Mt. Hikosan, 22.viii.1954, K. Yasumatsu. Paratypes: **Japan: Kyushu**: Mt. Hikosan, Fukuoka Pref., 5.viii.1940, K. Yasumatsu, 1♂ (ELKU). Lake Yamashita, Kokonoe-machi, Oita Pref., 9.ix.1997, R. Matsumoto, 1♀ (OMNH). Mt. Ariake-yama, Izuhara-machi, Tsushima Is., 24.vii.2001, R. Oomuta, 1♂ (TMUB). **Japan: Shikoku**: Mt. Ishizuchi-san, Omogo-mura, Ehime Pref., 17.viii.2002, M. Shiraishi, 1♀ (TMUB). Omogo, Omogo-mura, Ehime Pref., 16.viii.1951, T. Esaki, 1♂ (ELKU); 23.viii.1953, T. Edashige, 1♂ (TMUB); 23.ix.1999, A. Shimizu, 2♀ (TMUB). **Japan: Honshu**: Jomine Shrine, Yanô, Kamiizumi-mura, Saitama Pref., 3.viii.1994, T. Nambu, 1♂ (TMUB). Onouchi, Ogano-machi, Saitama Pref., 10.x.1992, T. Nambu, 1♀ (TMUB). Onagata, Yoshida, Saitama Pref., 18.viii.1988, T. Nambu, 6♀1♂ (TMUB), 1♀ (FSAG); 26.viii.1988 (2♀: TMUB, FSAG), 1, 3.viii.1994 (1♀: TMUB), 24,

26.viii.1995 (2♀: TMUB), 28.vii.2001 (2♂: TMUB), A. Shimizu. Riv. Ôchi-gawa, Ôtaki-mura, Chichibu, Saitama Pref., 6.ix.1970, T. Nambu, 2♀ (TMUB); 6.ix.1999, A. Shimizu, 1♀ (TMUB). Kawamata, Otaki, Chichibu, 18.viii.2005, A. Shimizu, 1♀ (TMUB). Mt. Komaga-take, 1050 m, Hakone, Kanagawa Pref., 8.viii.2005, A. Shimizu, 1♂ (TMUB). East of Fujikawaguchiko-machi, Minami-tsuru-gun, Yamanashi Pref., 5.viii.2006, H. Takahashi, 2♂ (TMUB). Mt. Sanage, Evergreen forest, Aichi Pref., deciduous forest, 8.ix.2002, P. Tripotin, 1♀. Jeollanamdo, Gurye-gun, Toji-myeon, Naedong-li, Piakol Valley, on wild wine flowers, 3.viii.2001, P. Tripotin, 1♀.

Etymology.—This species is named after the type locality.

Remarks.—This new species is similar to *I. pernix*, but the following characters distinguish them:

I. hikosanus	*I. pernix*
1. Lower anterolateral tubercle of pronotum slightly and roundly produced, almost concealed by disc in dorsal view (Fig. 1A).	Lower anterolateral tubercle of pronotum angulate, markedly projecting beyond disc in dorsal view (Fig. 1J).
2. Interantennal tubercle merging into upper frons, with median line finely impressed (Fig. 4B).	Interantennal tubercle abruptly raised from slightly depressed upper frons, with median line deeply and broadly impressed (Fig. 4A).

28.viii–3.ix.1992, T. Kanbe, Malaise trap, 1♀ (TMUB). Hio, Kanazawa-shi, Ishikawa Pref., 27.viii, 1998, Y.Tazaki, 1♂ (NSMT). Misaka-dani, Izumi-mura, Ono-gun, Fukui Pref., 13.ix.2002, H. Takahashi, 1♀ (TMUB). Kaizuka-shi, Izumi-katsuragisan, Osaka, 1.x.2000, R. Matsumoto, 1♀ (OMNH); 13–23.vii.2002 (1♂), 23.vii–2.viii.2002 (2♂), 2–10.viii.2002 (2♂), 20.viii–2.ix.2002 (1♀), 2–14.ix.2002 (1♀), 23.ix–2.x.2002 (1♀), 2–11.x.2002 (1♂), Malaise trap, R. Matsumoto, (OMNH). Kishiwada-shi, Izumi-katsuragisan, Osaka, 20–30.vi.2002 (1♀), 30.vi–13.vii.2002 (1♀1♂), 13–23.vii.2002 (2♀), 23.vii–2.viii.2002 (1♂), 2–10.viii.2002 (2♂), 10–20.viii.2002 (1♂), 23.ix–2.x.2002 (4♀), Malaise trap, R. Matsumoto, (OMNH). Six stage of Mt. Atago-yama, Ukyo-ku, Kyoto-shi, 27.viii.1987, A. Ichikawa, 1♀ (OMNH). Hanase Pass, Kyoto-shi, 10.ix.1999, R. Matsumoto, 1♀ (OMNH). Mimuro, Shingo-cho, Okayama Pref., 6.ix.1992, R. Matsumoto, 1♀ (OMNH). Kozagawa, Wakayama Pref., 20.ix.1957, S. Momoi, 3♀ (TMUB). Daisen, Tottori Pref. (Hôki), 19.viii.1932, S. Yasimoto, 1♂ (ELKU). **Korea**: Chungcheongnamdo, Keumsan, Poseoksa, 10.viii.1998 (1♀), 22.viii.1998 (1♀), 24.ix.2000 (1♀), ix.2001 (2♀), P. Tripotin, (FSAG). Kyeongsangnamdo, Jirisan, Hamyang-gun, Macheon-myon, Samjeong-li Jirisan, 700 m, 23–25.viii.2002 (4♀), 10–20.ix.2003 (1♂), Malaise trap, P. Tripotin, (FSAG). **CHINA**: Szechwan, Suifu, 1000–1500 m, 1–21.vi.1928, D. Graham, 1♀ (USNM).

Non-type material.—**Korea**: Chungcheongnamdo, Keumsan, Poseoksa, along trail in

Irenangelus nambui Shimizu, new species
(Fig. 2)

Female.—Length: Body 4.5–7.6 (5.5) mm; fore wing 4.7–6.9 (5.2) mm. *Coloration*: Body predominantly blackish brown to black and polished. Following ivory-white: clypeus and labrum laterally, mandible (apical portion brown), ventral margin of scape, maxillary and labial palpi, procoxa (basal portion more or less dark brown), protrochanter, and sometimes profemur, mid and hind coxae, trochanters, femora and tibiae partly. Remainder of fore leg light brown. Mid and hind legs predominantly brown, darker than fore leg, but somewhat lighter ventrally than dorsally. All tibial spurs ivory-white to yellowish light brown. Posterolateral margin of pronotum, lateral and posterior portions of metasomal terga, and posterior portions of metasomal sterna light brown to ferruginous. Wings hyaline, iridescent in certain lights, weakly infuscate along outer margins. Pterostigma dark brown. *Punctation*: Body devoid of punctures. *Pubescence and setae*: Body and legs with short, appressed white pubescence, longer and denser on lower frons, clypeus, lower pronotum, propleuron, mesopleuron, lower metapleuron, propodeum, and coxae. Upper

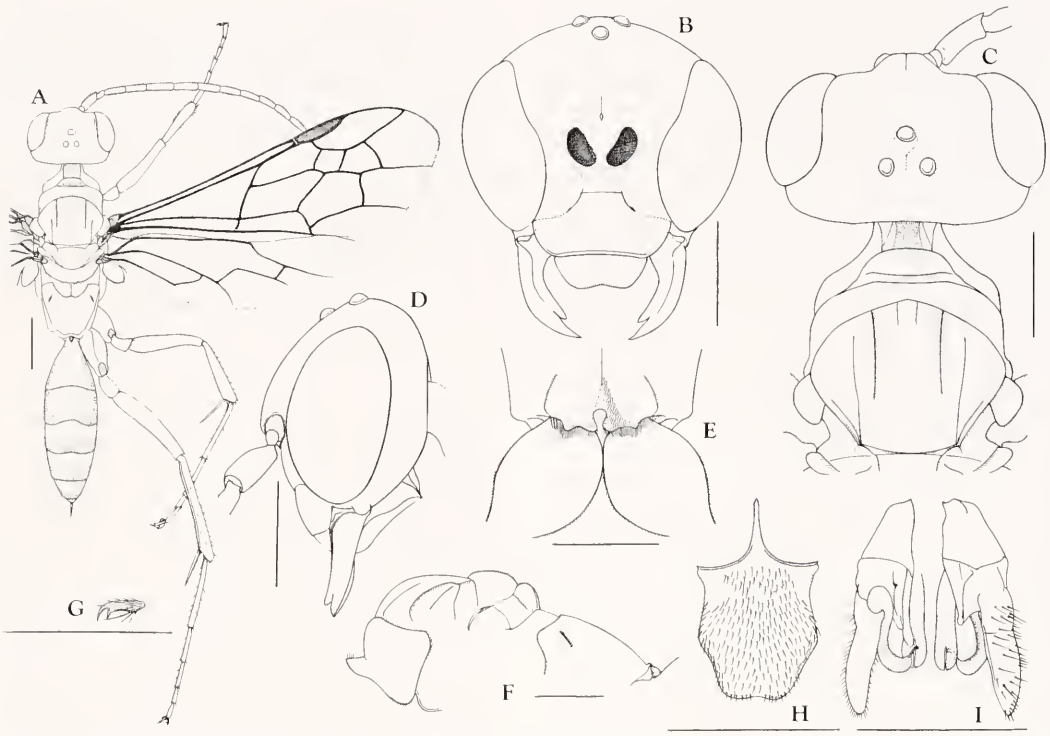

Fig. 2. *Irenangelus nambui* n. sp. (A–G, holotype female; H–I, paratype male from Japan). A, Whole body, dorsal view; B, head, frontal view; C, head, pronotum, and mesoscutum, dorsal view; D, head, lateral view. E, mesosternum and mesocoxa, ventral view; F, mesosoma, lateral view; G, right metatarsal claw, outer view; H, subgenital plate, ventral view. I, genitalia (left half, ventral view; right half, dorsal view). Scale lines: 0.5 mm.

frons, vertex, clypeus, labrum, mandible, apices of terga VI and sterna IV–V, and sternum VI with short pale setae. *Head*: 1.2× as broad as long. Vertex strongly convex in frontal view (Fig. 2B). Frons with interantennal area not tuberculate but slightly overhanging antennal sockets (Fig. 2D); median line impressed only on lower half. Antennocular line nearly transverse (Fig. 2C). Inner orbits slightly emarginate a little above middle, strongly divergent above. UID:MID:LID=9.8–10.1:10: 6.8–7.1 (10:10:6.9). MID 0.57–0.60 (0.60)× head width. Ocelli forming acute triangle, this area being scarcely raised. POL: OOL=1:2.5–3.6 (1:3.6). Clypeus slightly convex, 2.1–2.4 (2.2)× as broad as long; anterior margin truncate, weakly and arcuately emarginate (Fig. 2B); lateral sides arcuately convergent towards apex. Labrum 2.5–3.0 (3.0)× as broad as long; anterior margin arcuately emarginate. Mandible carinate laterally. Malar space short. Genae 0.3–0.4 (0.4)× eye width in profile, roundly receding in dorsal view. Scape sharply carinate beneath; lateral face slightly concave in dorsal view. Flagellomere I 2.9–3.5 (3.0)× as long as wide and 0.45–0.49 (0.47)× length of UID; flagellomeres I and II in ratio of 1:0.94–1.0 (1:0.98). *Mesosoma*: Pronotum short; anterior margin of disc arcuately convex in dorsal view, its anterolateral corner gently rounded (Fig. 2C); lower anterolateral tubercle not much swollen, being completely concealed by disc in dorsal view; posterior margin arcuate with small median notch. Mesoscutum with scutal groove sharply impressed anteriorly, becoming shallower and broader posteriorly, obsolete just an-

terior to scuto-scutellar sulcus; parapsidal sulcus finely impressed; posterolateral margin narrowly reflexed. Discs of scutellum and metanotum distinctly projecting (Fig. 2F), the latter being pyramidal. Posteromedian lobes of mesosternum short but bilobed, their inner lobes close to each other (Fig. 2E). Metapostnotum 0.7–0.9 (0.7)× length of metanotum at midline, with few very fine striae anteriorly and distinct longitudinal median groove. Propodeum weakly convex in profile (Fig. 2F), scarcely depressed along anterior margin, without lateral tubercle or infrastigmal tubercle (Fig. 2A); median groove obsolete; surface smooth, not striate. *Metasoma*: Slenderly fusiform. Tergum I abruptly narrowed, not petiolate or parallel-sided basally. *Legs*: Longer spur of metatibia 0.65–0.74 (0.69)× metatarsomere I. Tarsal claws sub-bifid: inner ray sub-parallel to outer ray, acute. *Wings*: Fore and hind wing venation as shown in Fig. 2A. Fore wing crossvein 2r-rs originating before middle of pterostigma. Crossvein cu-a originating slightly basad of point of separation of vein M+CuA. SMC2 rhomboid, receiving crossvein 1m-cu at basal 0.43–0.56 (0.52). SMC3 narrowed on vein Rs by 0.42–0.53 (0.51)× its length on vein M, 1.2–1.5 (1.3)× as long as SMC2 on vein M, 0.69–1.1 (0.87)× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at apical 0.54–0.66 (0.58). Hind wing crossvein rs-m almost straight, oblique to vein M. Crossvein cu-a forming angle of 135–140° to vein A.

Male.—Very similar to female. *Length*: Body 3.9–8.3 mm; fore wing 3.7–6.5 mm. *Head*: 1.2× as broad as long. UID:MID:LID=9.9–10.1:10:7.0–7.7. MID 0.57–0.60× head width. POL:OOL=1:2.1–3.1. Clypeus 2.3–2.5× as broad as long. Labrum 2.6–3.2× as broad as long. Gena 0.3–0.4× eye width in profile. Flagellomere I 2.2–2.7× as long as wide and 0.38–0.43× as long as UID; flagellomeres I and II in ratio of 1:0.96–1.1. *Mesosoma*: Metapostnotum 0.8–1× length of metanotum at midline. *Legs*: Longer spur of metatibia 0.66–0.73× metatarsomere I. *Wings*: SMC2 receiving crossvein 1m-cu at basal 0.44–0.60. SMC3 narrowed on vein Rs by 0.44–0.73× its length on vein M, 1.1–1.6× as long as SMC2 on vein M, 0.64–1.4× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at apical 0.50–0.66. *Subgenital plate* (Fig. 2H): Broadened medially; apical margin slightly emarginate or truncate; ventral surface covered with minute setae. *Genitalia* (Fig. 2I): Paramere without strong setae apicomedially; parapenial lobe short, not attaining apex of aedeagus.

Distribution.—Japan and Korea (Fig. 6).

Type material.—Holotype ♀ (TMUB), Nageishi Pass, Higashi-Mikabo, Gunma Prefecture, 28.viii.1986, T. Nambu. Paratypes: **Japan: Honshu**: Showa, Mt. Hakase, 1000 m, Beech forest, Fukushima Pref., 29.vi–26.vii.1998 (1♂), 27.vii–23.viii.1998 (6♀7♂), 24.viii–19.ix.1998 (1♀2♂), Malaise trap, T. Muroi, (TMUB). Imperial Palace, Chiyoda-ku, Tokyo, 28.v.1999, T. Nambu, 1♂ (TMUB). Mt. Komaga-take, 1000–1300 m, Hakone, Kanagawa Pref., 11.vii.2000 (1♂), 30.viii.2000 (1♀), H. Nagase, (TMUB); 18.vii.2001 (1♀7♂: TMUB; 1♂, FSAG), 1.viii.2001 (2♂: TMUB), A. Shimizu. Takekurabe-yama, Maruoka-cho, Fukui Pref., 5.ix.1994, Y. Haneda, 1♀ (TMUB). Akausagi-yama, Ohno-shi, 23.ix.1974, Y. Haneda, 1♀ (FSAG). Shitara, Beech forest, 900 m, Uradani, Aichi Pref., 25–31.vii.1994 (1♂), 29.viii–4.ix.1994 (1♂), Malaise trap, K. Yamagishi, (TMUB); 29.viii–4.ix.1994, Emergence trap, K. Yamagishi, 1♀1♂ (TMUB); 19–25.ix.1994, Pan trap, K. Yamagishi, 1♀ (TMUB); 1–7.viii.1994 (1♂: TMUB), 22–28.viii.1994 (1♀1♂: TMUB; 1♀, FSAG), Malaise trap, T. Kanbe. Asahi, Yawata, 650 m, Deciduous forest, 17–26.vi.1998 (2♂), 12–21.viii.1998 (1♀1♂), 15–25.ix.1998 (1♀), Malaise trap, M. Ozawa, (TMUB). Mt. Sanage, Evergreen forest, Aichi Pref., 28.viii–3.ix.1992, Emergence trap, K. Shima, 1♀ (TMUB); 4–10.ix.1992, Malaise trap, T. Kanbe, 1♀ (TMUB); 16–22.ix.2002, Malaise trap, M. Kiyota, 1♂ (TMUB). **Korea**: Kyeongsangnamdo, Jirisan, Hamyang-gun, Macheon-myon, Samjeong-li, 700 m, 35°20′55N 127°38′21E, Malaise trap, 10–20.ix.2003, P. Tripotin, 2♀2♂ (FSAG).

Etymology.—This species is named in honor of the provider of the holotype specimen.

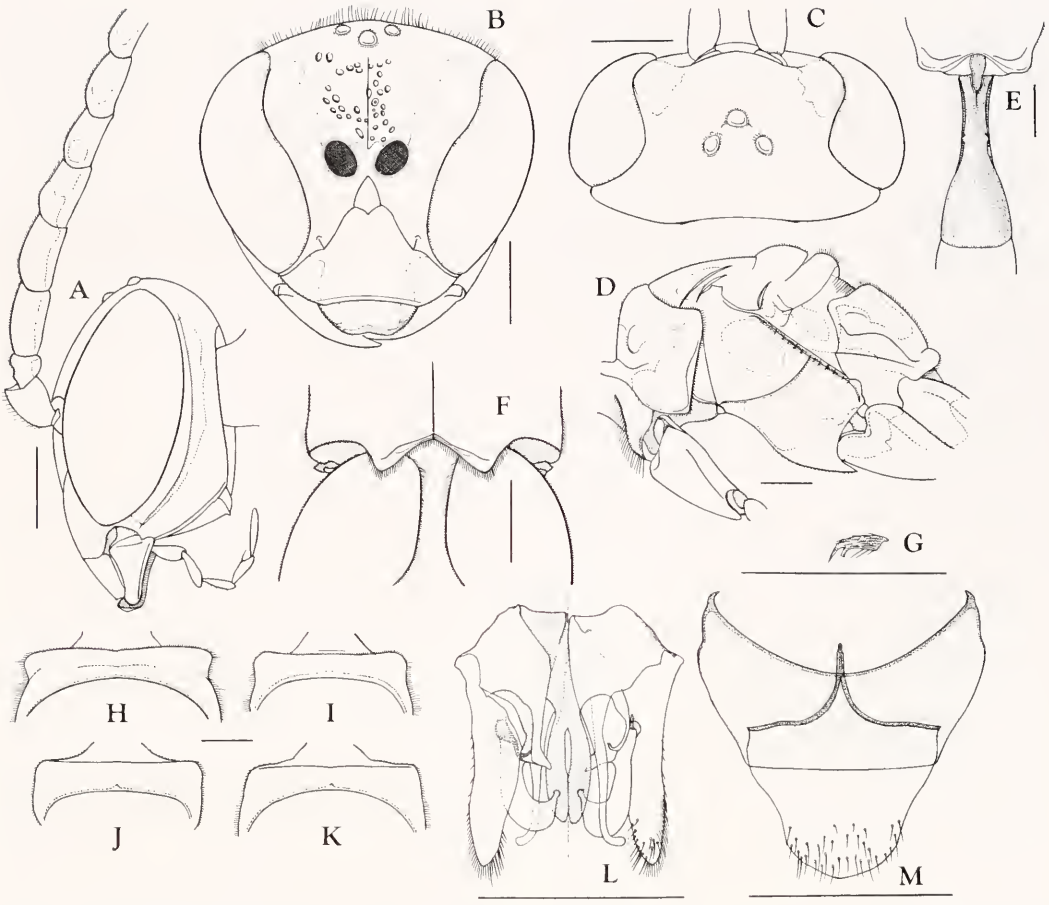

Fig. 3. *Irenangelus punctipleuris* n. sp. (A–G, I, holotype female; H, J–K, paratype females: H, from Sulawesi; J, from Brunei; K, from Japan); L–M, paratype male from Japan). A, Head and antenna, lateral view; B, head, frontal view; C, head, dorsal view; D, mesosoma, lateral view; E, metasomal tergum I, dorsal view; F, mesosternum and mesocoxa, ventral view; G, right metatarsal claw, outer view; H–K, pronotum, dorsal view; L, genitalia (left half, dorsal view; right half, ventral view); M, sternum VII and subgenital plate, ventral view. Scale lines: 0.5 mm.

Remarks.—In *Irenangelus* this species is unique in its predominantly dark brown to black body and wholly transparent wings.

Irenangelus punctipleuris Wahis, new species

(Figs 3, 4C–F, 5B–C)

Female.—Length: Body 8.1–12.4 (10.0) mm; fore wing 6.2–9.3 (7.9) mm. *Coloration*: Head, mesosoma and coxae black with following bright yellow: clypeus and labrum (lateral portions black), frons between and below antennal sockets, upper frons along inner orbit and gena along outer orbit broadly, scape and pedicel (dorsal faces dark brown to black), pronotal disc (lateral margin black), ventral and posterolateral margins of pronotum broadly, posteromedian elliptic spot and lateral streak on mesoscutum, median spot on scutellum, metanotal disc, oblong spot on upper mesopleuron, this spot being sometimes obsolete, two large spots on lower mesopleuron, these often being continuous (Figs 4E–F), median triangular and lateral longitudinal marks on propodeum, these being continuous posteriorly, oblique spot on upper metapleuron, this spot being

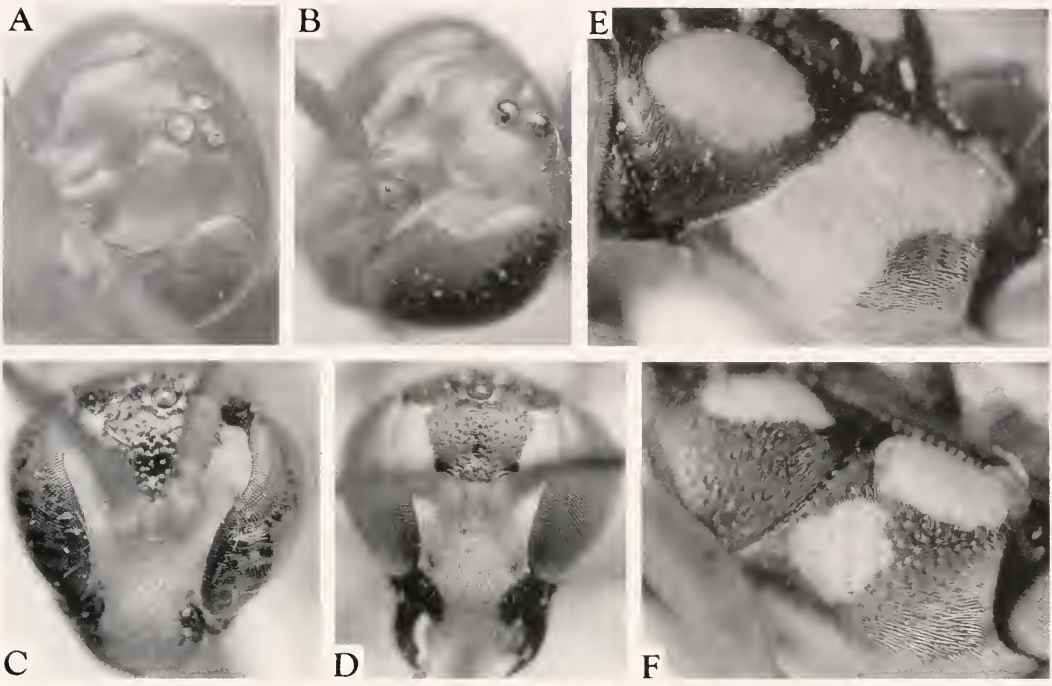

Fig. 4. Female head (A–D) and mesopleuron (E–F) of *Irenangelus* (A–B, dorsolateral view; C–D, frontal view; E–F, lateral view). A, *I. pernix* Bingham from Bali, Indonesia; B, *I. hikosanus* n. sp., holotype; C–F, *I. punctipleuris*, n. sp. (C, E, holotype; D, F, paratype from Japan).

sometimes obsolete, posterodorsal mark on lower metapleuron, this being continuous with lateral propodeal mark, apical greater parts of coxae, and sometimes side of metanotum and anterior portion of metapostnotum. Following reddish brown: flagellomeres I–IV or –X ventrally (remainder of flagellum dark brown to black), maxillary and labial palpi, trochanters (basally dark brown to black), femora (dorsolateral portion of profemur and sometimes ventral portions of meso- and metafemora bright yellow; sometimes all femora dark brown ventrally and/or laterally), tibiae (protibia bright yellow dorsolaterally; sometimes dorsal portion of mesotibia and basidorsal

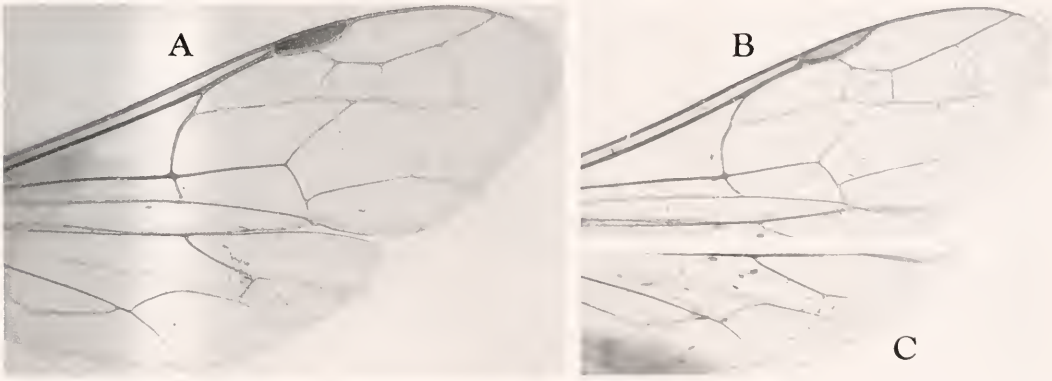

Fig. 5. Female wings (A, fore and hind wings; B, fore wing; C, hind wing). A, *I. hikosanus* n. sp., holotype; B–C, *I. punctipleuris* n. sp., paratype from the Philippines.

I. hikosanus H
I. nambui N
I. punctipleuris P

portion of metatibia dark brown to black), tarsi, and metasoma (tergum I dark brown to black anterodorsally and sublaterally; terga II–IV sometimes becoming darker dorsally). Posterolateral margin of mesoscutum, tegula, and wing bases yellowish brown. Mandible black; apical 1/3 dark rufous. Wings hyaline, iridescent in certain lights, weakly infuscate along outer margins. Pterostigma light to dark brown. *Punctation*: Upper frons (Figs 4C–D), vertex between eye and ocellus, pronotum, mesoscutum, discs of scutellum and metanotum, mesopleuron (Figs 4E–F), and lower metapleuron with irregularly-spaced, shallow punctures, these being larger and denser along median line of frons and scutal groove, and sometimes on mesopleuron. *Pubescence and setae*: Body and legs with short, appressed, white to pale brown pubescence but devoid of long bristly setae; vertex, mandible, propleuron, lateral side of pronotal disc, mesopleuron, metanotum, and posterolateral portion of propodeum with short, dense, white to pale brown setae. *Head*: 1.1–1.2 (1.2)× as broad as long. Vertex strongly convex in frontal view (Fig. 3B). Frons without interantennal tubercle (Fig. 3A); median line finely impressed from interantennal area close to anterior ocellus. Antennocular line slightly depressed nearby antennal base (Fig. 3C). Inner orbits distinctly emarginate at upper 1/3, strongly convergent below. UID: MID:LID=8.5–9.4:10:5.6–6.5 (9.3:10:5.9). MID 0.59–0.63 (0.61)× head width. Ocelli forming slightly acute triangle, this area being slightly raised. POL:OOL=1:1.6–2.5 (1.9). Clypeus feebly convex, 1.6–1.9 (1.8)× as broad as long; anterior margin truncate, weakly and arcuately emarginate (Fig. 3B); lateral sides strongly convergent towards apex. Labrum 2.0–2.3 (2.2)× as broad as long; anterior margin with small median notch. Malar space very short (Fig. 3A). Mandible sharply carinate laterally. Gena 0.4–0.5 (0.4)× eye width in profile, feebly rounded in dorsal view. Scape carinate on apical half ventrally; lateral face flattened but scarcely concave in dorsal view. Flagellomere I 2.1–2.4 (2.4)× as long as wide and 0.38–0.43 (0.38)× length of UID; flagellomeres I and II in ratio of 1:0.84–1.0 (0.94). *Mesosoma*: Pronotum short; anterior margin of disc almost straight in dorsal view, its lateral corner sub-angulate, but degree of angulation variable (Figs 3H–K); lower anterolateral tubercle not much swollen, being concealed by disc in dorsal view; posterior portion narrowly but distinctly depressed along posterior margin, the latter being arcuate. Mesoscutum with scutal groove shallowly impressed on anterior 1/4–3/4; parapsidal sulcus appearing as a fine, raised line; posterolateral margin narrowly reflexed. Discs of scutellum and metanotum strongly raised (Fig. 3D). Metapostnotum 0.59–1.0 (1.0)× length of metanotum at midline, deeply sunken between metanotum and propodeum, with fine, transverse striae anteriorly and short oblique striae posteriorly. Posteromedian lobes of mesosternum triangularly produced, their apices removed from each other (Fig. 3F). Upper metapleuron finely and obliquely striate. Propodeum short, barely convex in profile (Fig. 3D), deeply depressed along anterior margin, without lateral tubercle; infrastigmal tubercle weak; surface finely and transversely striate, with weak to rudimentary median groove. *Metasoma*: Much slenderer than mesosoma. Tergum I gradually narrowed and petiolate or parallel-sided basally (Fig. 3E). *Legs*: Longer spur of metatibia 0.63–0.72 (0.68)× length of metatarsomere I. Tarsal claws bifid; inner ray of claw truncate (Fig. 3G). *Wings*: Fore and

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Fig. 6. Map showing the known distribution of *Irenangelus hikosanus*, *I. nambui*, and *I. punctipleuris*. In Japan only certain localities of specimens, including type localities, have been selected for *I. hikosanus* and *I. nambui*.

hind wing venation as shown in Figs 5B and C, respectively. Fore wing crossvein 2r-rs originating slightly before middle of pterostigma. Crossvein cu-a usually originating at or slightly basad of point of separation of vein M+CuA. SMC2 almost rectangular, receiving crossvein 1m-cu at basal 0.43–0.57 (0.54). SMC3 narrowed on vein Rs by 0.75–0.85 (0.84)× its length on vein M, 1.3–1.8 (1.8)× as long as SMC2 on vein M, 1.2–1.8 (1.8)× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at basal 0.39–0.61 (0.50). Hind wing crossvein rs-m almost vertical to vein M. Crossvein cu-a forming angle of approximately 150° to vein A.

Male.—Very similar to female. *Length*: Body 6.7–8.4 mm; fore wing 5.7–7.0 mm. *Head*: 1.2× as broad as long. UID:MID:LID=9.0:10:6.7–7.3. MID 0.62–0.65× head width. POL:OOL=1:1.9–2.1. Clypeus 2.0× as broad as long. Labrum 2.1–2.2× as broad as long. Gena 0.4–0.5× eye width in profile. Flagellomere I 2.3–2.4× as long as wide and 0.32–0.35× UID; flagellomeres I and II in ratio of 1:0.87–0.90. *Mesosoma*: Metapostnotum 0.75× length of metanotum at midline. *Legs*: Longer spur of metatibia 0.72× metatarsomere I. *Wings*: SMC2 receiving crossvein 1m-cu at basal 0.42–0.55. SMC3 narrowed on vein Rs by 0.77–0.78× its length on vein M, 1.4–1.7× as long as SMC2 on vein M, 1.3–1.5× as long as SMC2 on vein Rs, receiving crossvein 2m-cu at basal 0.45–0.67. *Subgenital plate* (Fig. 3M): Lateral sides gradually convergent towards apex; apical margin sub-triangularly produced; ventral surface with minute setae apically. *Genitalia* (Fig. 3L): Paramere with strong setae apicomedially; parapenial lobe long and slender, decurved apically, extending beyond apex of aedeagus.

Distribution.—From Japan through the Philippines and Malaysia to India and Sri Lanka (Fig. 6).

Type material.—Holotype ♀ (ZMUC), Philippines, Balabac Dalawan Bay, 7.x.1961, Noona Dan Exp. 61–62. Paratypes: **Philippines**: Tawi Tawi, Tarakawan, north of Batu Batu, 4.xi.1961 (1♀: ZMUC), 10.xi.1961 (1♀: FSAG), 12.xi.1961 (1♀: ZMUC), Noona Dan Exp. 61–62. **Brunei**: Ulu Temburong, Base camp hut, 300 m, 115 16′E 4 26′N, 16.ii–9.iii.1982, M. C. Day, 2♀ (BMNH, FSAG). **Sulawesi**: Central Sulawasi, Napu-valley, 100 km S/O, Palu, near Lore-Lindu National Park, 9.ii.2001, A. -M. Klein, 1♀ (FSAG). Utara, Dumoga-Bone Nat. Park, ii.1985, 1♀ (BMNH). **Bali**: W. Bali, near Negara, rainforest above Batuagung, 550 m, 4–6.xii.1911, C. v. Achterberg, 1♀ (RMNH). **Java**: W. Java, Djampang-Tengah, Mrs. Walsh, 1♀ (RMNH). **Borneo**: Sarawak, S.W. Gunung Buda, 64 km S. Limbang 4 13′N 114 56′E, 8–15.xi.1996, Malaise trap, S. L. Heydon & S. Fung, 1♀ (UCDC). **Malaysia**: S. E. Sabah, Danum Valley Field C., 117 48′E 4 58′N, x–xii.1986, P. Eggleton, 4♀ (BMNH), 1♀ (FSAG). S. E. Sabah, near Danum Valley Field, ca.150 m, 26.v–20.vi.1987 (4♀: RMNH; 3♀: FSAG), 20.vi–12.vii.1987 (1♀: RMNH), 13.ix–4.x.1987 (1♀: RMNH), Malaise trap, C. v. Achterberg & D. Kennedy. S. W. Sabah, near Long Pa Sia (West), 1020 m, 25.xi–9.xii.1987, Malaise trap, C. v. Achterberg, 1♀ (RMNH). S. W. Sabah, near Long Pa Sia (East), 1000 m, 1–13.iv.1987 (1♀), 25.xi–9.xii.1987 (1♀), Malaise trap, C. v. Achterberg, (RMNH). Pasoh Forest Reserve, Negeri S., 22.vii.1978 (1♀: AEIC), 7.ix.1978 (1♀: FSAG), 6.xi.1978 (1♀: AEIC), 8.i.1979 (1♀: AEIC), P. & M. Becker. Bukit Kutu, 30.i.1930, H. T. Padgen, 1♀ (BMNH). **India**: U. P. Garjia, 610 m, 26–29.iv.1969, Gupta, No. 335, 1♂ (FSAG). S. India, Madras ST., Anamalai Hills, 3500 f, v.1964, P. S. Nathan, 1♀ (CNC). Kerala, Periyar A. Sanctuary, 5–15.x.1979, 1♀ (BMNH). **Sri Lanka**: Kandy District, Udawattakele Sanctuary, 1800 f, 1–3.ix.1980, Malaise trap, K. V. Krombein et al., 1♀ (FSAG). **Japan**: Kawamata, Ôtaki-mura, Chichibu, Saitama Pref., 30.vi–1.vii.2004, A. Shimizu, 1♀ (TMUB). Marunomachi, Nirasaki-shi, Yamanashi Pref., 27.vi–5.vii.2005, Malaise trap, K. Hosoda, 1♂ (TMUB). Kanegasaki-chô, Tsuruga-shi, Fukui Pref., 3.vii.2001, H. Takahashi, 1♀ (TMUB).

Etymology.—The species name is derived from the punctate mesopleuron; puncti- (punctate) + pleuris (pleuron).

Remarks.—The present species is similar to "*Ceropales*" *tenuatus* Turner 1910 occurring in Australia in that 1) the flagellum is crenulate; 2) all tarsal claws are bifid; 3) the frons is devoid of an interantennal tubercle;

and 4) the metasomal tergum I is gradually narrowed and petiolate or parallel-sided basally. However, this new species is easily distinguished from the latter by the almost entirely rufous metasoma and the distinctly punctate mesopleuron.

ACKNOWLEDGMENTS

We thank Emeritus Professor R. Ishikawa (Tokyo Metropolitan University) and Dr N. Springate (Natural History Museum, London) for reviewing our manuscript and providing critical comments. For the gift or loan of specimens, our thanks are also due to the following: M. C. Day, T. Edashige, T. Esaki, Y. Haneda, K. Hosoda, L. S. Kimsey (UCDC), K. V. Krombein (USNM), R. Matsumoto (OMNH), S. Momoi, H. Nagase, T. Nambu, R. Oomuta, A. Shinohara (NSMT), M. Shiraishi, O. Tadauchi (ELKU), H. Takahashi, Y. Tazaki, P. Tripotin, L. B. Vilhelmsen (ZMUC), K. Yamagishi, Y. Yasimoto, and K. Yasumatsu.

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Natural History and Larval Behavior of the parasitoid *Zatypota petronae* (Hymenoptera: Ichneumonidae)

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Abstract.—The koinobiont ectoparasitoid *Zatypota petronae* Gauld (Ichneumonidae) parasitizes medium-sized immatures of the cobweb spider *Theridion evexum* Keyserling (Theridiidae). *Zatypota petronae* apparently attacks the spider inside its retreat. An egg is glued on the antero-lateral dorsal section of the spider's abdomen. First-instar larvae remain partially inside the egg chorion which is attached to the spider's abdomen. In later instars, a layer of a brownish material (saddle), to which the 7th and 8th abdominal segments of the larva adhere ventrally, anchors the larva to the spider. In the last instar the saddle includes the egg chorion and the shed exoskeletons of previous instars. A row of retractile, dorsal protuberances, crowned with hooklets, is present on abdominal segments 1 to 8 of the final-instar larva. The larva uses the hooklets to grab silk lines of the retreat of the spider's web. Hanging on the spider's web the larva kills the spider and sucks out its body tissues. Then the larva pushes vigorously laterally with its head against the spider's corpse, and alternately presses the corpse against the saddle. These movements, in combination with peristaltic movements, free the larva from the saddle that falls to the ground with the dead spider. The larva then constructs its pupal cocoon. Prior to cocoon construction, the larva induces the spider to reinforce the retreat by adding more threads. Parasitism rate and host behavior are also described.

The polysphinctine pimplines are koinobiont ectoparasitoids of spiders in several families (Nielsen 1923, 1932, Fincke et al. 1990, Hanson and Gauld 1995, Gauld et al. 1998). Nielsen (1923, 1932) described in detail the behavior of the larvae and hosts of several European polysphinctine species. The parasitism rates and life cycle of *Hymenoepimecis robertsae* Gauld on the neotropical tetragnathid *Nephila clavipes* (L.) was described by Fincke et al. (1990). However, larval behavior of neotropical polysphinctine wasps has been described in detail for only one species, *H. argyraphaga* Gauld on the tetragnatid *Plesiometa argyra* (Walker) (Eberhard 2000a, 2000b, 2001).

Parasitoid wasps of the cosmopolitan speciose polysphinctine genus *Zatypota* Förster parasitize spiders in at least five families (Dictynidae, Agelenidae, Tetragnathidae, Araneidae and Theridiidae) (Shaw 1994, Gauld et al. 1998). In the neotropics the only two host records were *Theridion* species: *T. contreras* Levi for an unidentified *Zatypota* species (Jiménez 1987) and *T. evexum* Keyserling for *Z. petronae* Gauld (Barrantes and Weng in press).

The larval behavior of *Zatypota* sp. (Jiménez 1987) differs in some aspects from that of European polysphinctine species (Nielsen 1923, 1932) and *H. argyraphaga* (Eberhard 2000a). The larva of *Zatypota* sp. was said to hold on to the spider by biting the dorsum or sides of the anterior section of the spider's abdomen. This description is likely wrong as detailed descriptions of the behavior of the larva of *Z. albicoxa*

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(Nielsen 1923) and the larva of *H. argyraphaga* (Eberhard 2000a) show that some posterior segments of the larvae lodge ventrally in a "saddle", probably coagulated spider's hemolymph, that adheres tightly to the spider's abdomen (Nielsen 1923, Eberhard 2000a). There is no further information on the biology of larvae of this *Zatypota* species. Here we describe the intensity of parasitism and behavior of the larva of *Z. petronae* and its host *T. evexum*. We describe for the first time how a polysphinctine larva frees itself from the spider's corpse.

MATERIALS AND METHODS

Field observations were made from October 2005 to October 2006 in a 250 m^2 plot in the understory of a middle-elevation wet forest patch (9° 54'N, 84° 03'W; elevation 1200 m), the Reserva Biológica Leonel Oviedo on the Universidad de Costa Rica campus, San José Province, Costa Rica. All spiders (or nearly so) from third-forth instar outside the egg sac to adults were checked for parasites every two weeks; most spiderlings disperse from the mother's web at fourth instar. The small eggs and early instar larvae probably went undetected.

Theridion evexum constructs most webs between 0.20 to 1.5 m above the ground (Barrantes and Weng in press), making it possible to find practically all webs. Additionally, we collected seven parasitized spiders and kept them on their webs indoors to observe the behavior of larvae and spiders. In two cases we transplanted the plant on which the parasitized spider had constructed its web indoors, allowing us to observe the larva and host behavior with little disturbance. The complete larval development was not observed in all cases, so sample sizes are not always the same. Behavior and morphological features of more than 10 larvae were observed under a dissecting microscope. Video recordings of behavior were made using a Sony DCR – VX 1000 camcorder with +5 close-up lenses. Drawings of larval behavior were traced from video recordings. Voucher specimens of wasps and spiders were deposited in the Museo de Zoología of the Universidad de Costa Rica. Wasp species names follow Gauld et al. (1998).

RESULTS

Percentage of parasitism.—Only juveniles of *T. evexum* were found to be parasitized by *Z. petronae*. A second instar larva was feeding on a juvenile spider, possibly a third instar. However, final instar larvae were found feeding on large immature spiders, possibly juveniles of fourth to fifth instars. The parasitism in *T. evexum* was very low (mean percentage of parasitism/census = 1.39%, SD = 1.80, n = 53 biweekly censuses). The reproduction in *T. evexum* is extremely seasonal, and the abundance of immature spiders (4th instar or larger) susceptible to attack by *Z. petronae* increased in March and declined drastically through August (Fig. 1). Between September and February the population consists, first, of mature females, and then of very small spiderlings (Fig. 1). Parasitized spiders occurred primarily from March through August.

Spider web and wasp attack.—The web of *T. evexum* includes a folded leaf that forms a conical retreat, with a tangle in front of the retreat opening, and long viscid threads extending from the tangle to other leaves (Barrantes and Weng in press). An additional tangle is constructed by the spider inside on the upper side of the retreat.

We witnessed one attack by a female *Z. petronae* wasp. The wasp approached the web and hovered in front of the spider's retreat opening. The wasp then flew inside the retreat. A few seconds later, the spider, with the wasp perched on its dorsum, dropped about 10 cm below the retreat, and hung on its dragline. They struggled for a few seconds and then the wasp flew out of sight. The spider began to climb towards the retreat but after advancing

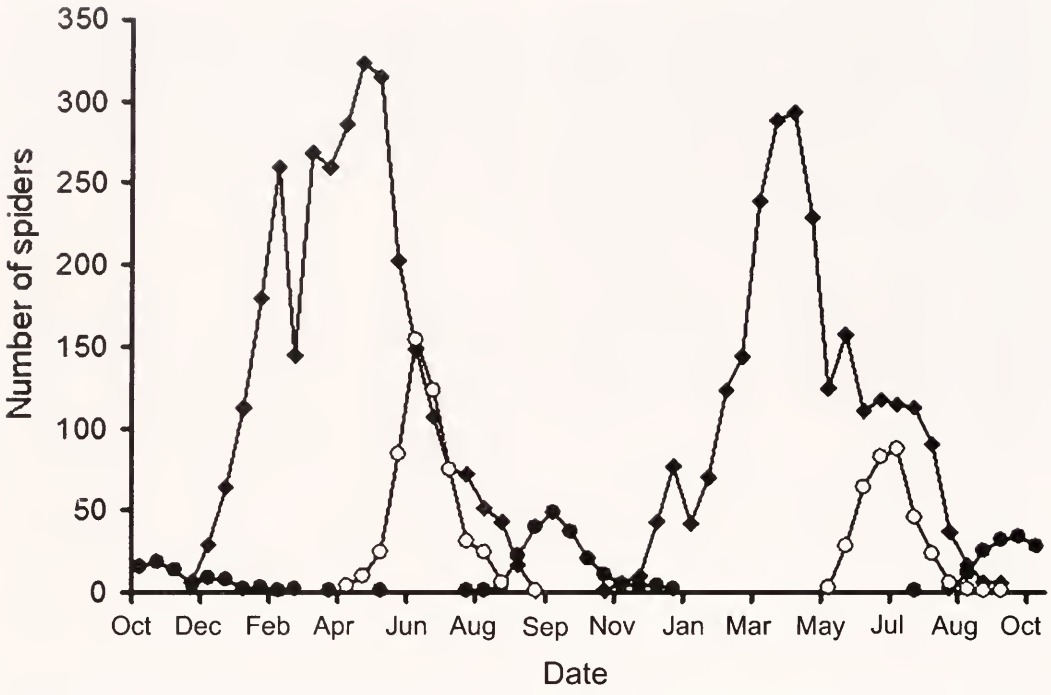

Fig. 1. Temporal changes in the number of immature spiders (black rhombus), males (open circles), and reproductive females (black circles) of *T. evexum*.

about four centimeters, it became paralyzed and fell back, motionless for about 10 min, dangling from its dragline. The spider recovered its motion slowly, and with clumsy movements cleaned some of its legs before ascending to the retreat. When we returned, 30 min later, the spider had fully recovered its mobility. We did not ascertain whether the spider had an egg on its abdomen.

Larvae.—We observed one egg of *Z. petronae* glued on the antero-lateral dorsal section of the abdomen of a spider collected in the field, a first instar larva emerged about four hours later. All eleven larvae of different instars checked under the dissecting microscope were attached by their rear end to the cuticle of the antero-lateral surface of the spider's abdomen (Fig. 2A).

The first instar larva (n = 3) had its posterior end lodged inside the egg chorion, with its head, thorax, and some abdominal segments protruding; the chorion remained attached to the spider. In the "second" instar, larvae (n = 5) were completely outside the collapsed, flattened egg chorion that was embedded in an apparently rigid, semitransparent layer of brownish material (Fig. 2B) (the "saddle" of Nielsen 1923). The ventral surface of two or three posterior abdominal segments rested on the saddle. In subsequent instars, the cuticles of the previous molts became incorporated into the saddle as they adhered to its upper surface, against the ventral surface of the larva. The egg chorion was near the spider's surface, but not in contact with it. The saddle was attached by a short pedicel to the spider's abdomen (Fig. 2B), and the larva's abdominal segments 7 and 8 secured it to the saddle. Feeding scars were observed on the nearby dorsal and lateral surface of the spider's abdomen (Fig. 2B).

In the final instar, larvae had dorsal, two-lobed, retractable tubercles on eight abdominal segments (1st to 8th); these structures were absent in previous stages.

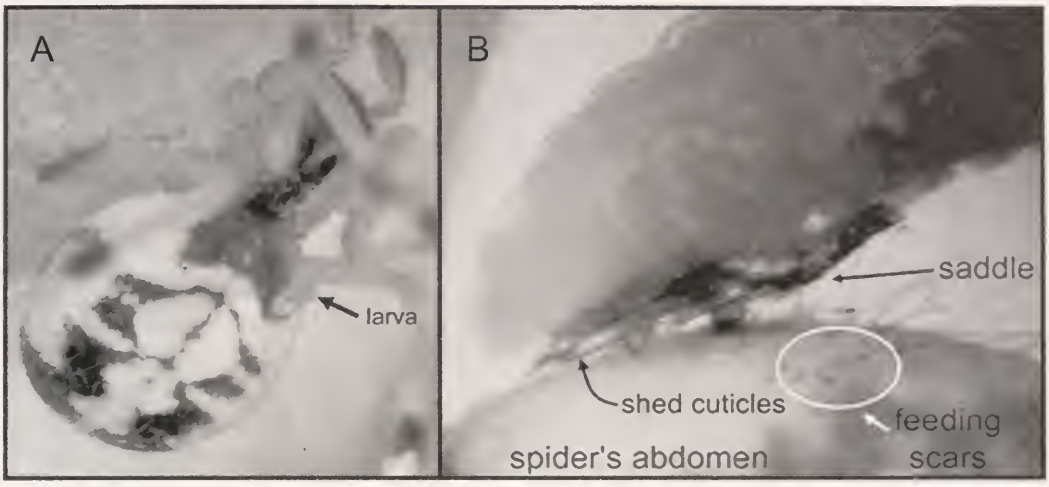

Fig. 2. Larva of *Z. petronae*: A- Second instar larva attached to the antero-lateral surface of the spider's abdomen. B- Penultimate larva with the saddle attached to the spider's abdomen. The shed cuticles of previous molts are visible under the larva. Feeding scars (black dots) are also visible on the surface of the spider's abdomen. (Photo of a specimen in alcohol).

When extended, the tubercles were crowned with a circle of tiny hooks that allowed the larva to grab the threads of the spider's web inside the retreat. The larva could extend or retract independently each lobe of the tubercle, and the tubercles could be retracted rapidly and completely into a pocket. Based on size and morphology, we discerned three instars in the larvae of this wasp. However, the saddle of what we thought was a second instar larva included the chorion and the shed cuticles of two molts. Hence, further observations are needed to confirm the number of instars.

The final instar larva spent about 18 h attached to the spider (n = 2), three to six hours after removing the saddle and prior to cocoon construction (n = 5), and nearly 18 h constructing the cocoon (n = 1). The duration of the larva inside the cocoon before pupation was not recorded. One penultimate instar larva molted during the night and the next morning hung from lines near the roof of the retreat with its dorsal hooks, and fed on the spider for about eight hours. During approximately the first four hours the spider's legs moved slightly, but later we could not detect any movement. The larva fed first on the spider's abdomen, then on its cephalothorax. When discarded, the spider's carcass was nearly completely empty; even its legs were almost transparent. The larva was thus capable of extracting nearly completely the spider's internal tissues, presumably using capillarity (Eberhard et al. 2006).

Dislodging the saddle.—After the larva had finished feeding, it began to free itself from the saddle while hanging inside the spider's retreat. The process, which lasted about two hours, included three types of movement: pressing the spider carcass against the saddle, pushing the spider carcass laterally, and peristaltic movements of the larva's abdominal segments. The pressing and peristaltic movements seemed to be more frequent and intense just before the spider carcass and saddle were completely removed.

Pressing movements: The ventral side of the larva's head pushed on the spider's anterior end, steadily pressing the spider's carcass against the saddle until it bent almost completely over the saddle (Fig. 3A, B). The larva then released the pressure completely as it moved its head to

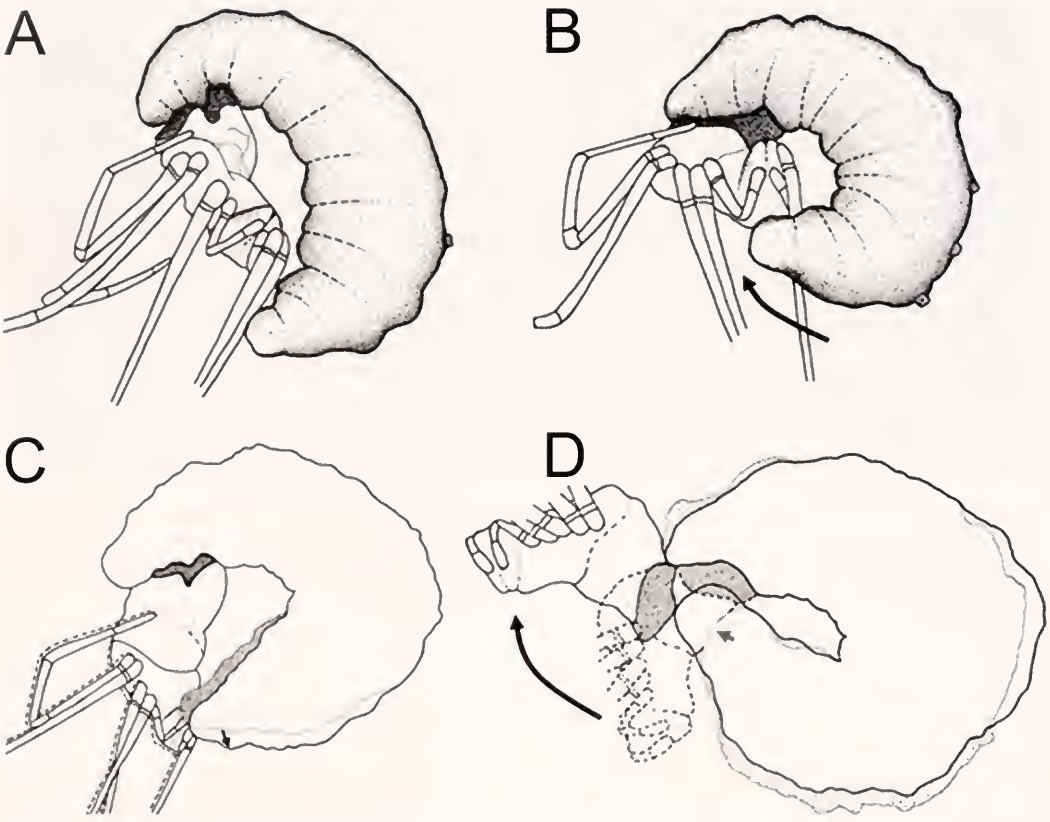

Fig. 3. Movements of the spider to free itself from the saddle (traced from video images). Pressing movement: the larva places its head near the spider's chelicerae (A) and presses the spider carcass against the saddle (B). Lateral pushing: the larva places its head on the anterior tip of the spider carcass and pushes it laterally (C). A backward final push completely dislodges the saddle from the larva (D); the grey arrow shows the position of the larva's head tip before pushing the saddle. Dotted and dashed lines represent the initial positions of the larva and the spider's carcass respectively.

the initial position, and then either made another pressing movement or pushed the spider's carcass laterally (see below).

Lateral pushing: The larva bent ventrally until the lateral section of its head contacted the legs and/or cephalothorax of the dead spider, and then pushed laterally (Fig. 3C). Then it moved its head back slightly, maintaining contact with the carcass, and pushed laterally again. The larva pushed repeatedly up to 10 times before reorienting its head; the complete carcass moved visibly with each push by the larva. The larva often placed its head on the opposite side of the spider during successive pushing bouts. During the last three pushing bouts the larva's head was oriented at about 30° to its longitudinal axis and contacted the saddle, rather than the spider and the force exerted by the pushing movement was toward the rear of the larva's body rather than laterally (Fig. 3D).

Peristaltic movements: Peristaltic waves moved posteriorly along the larva's abdominal segments during pressing and pushing movements. The last segment stretched extensively backward as the wave reached it. The peristaltic waves were strongest during the last pressing and lateral movements of the larva.

Final events: As soon as the saddle was released the larva rubbed its head against the ventral surface of the segments that

had been connected to the saddle, which were covered with a mucilaginous substance. The small processes on the ventral larval segments that are inserted in the saddle in other polysphinctines (the "taps" of Nielsen 1923, Eberhard 2000a) were not visible in the *Z. petronae* larva at the moment the saddle was released. However, examination of two saddles under the dissecting and compound microscopes showed a wedge-like depression inside the saddle. This depression was likely produced by an abdominal projection that anchored the larva to the saddle.

Cocoon construction.—One larva of *Z. petronae* began cocoon construction at about 18:30 h inside the spider's retreat, after resting for nearly two hours. We did not follow cocoon construction in detail, but our incomplete observations indicate that the behavior was quite similar to cocoon construction by *H. argyraphaga* (Eberhard 2000a), except that no suspension line was built. Construction lasted nearly 18 h (N=1). It began with the larva hooked by its dorsal tubercles to the silk threads of the tangle inside the retreat (Fig. 4A).

The larva built the cocoon by attaching a silk line (or lines) produced from its head to the tangle of threads made by the spider, and pulling its head from this point to the next attaching point, which was either another tangle thread or one of its own previously produced lines. Cocoon construction began around the posterior portion of the larva (Fig. 4B) and then gradually extended upward until it enclosed the larva. The first silk lines around the larva formed a loose, fluffy mass (Fig. 4C), but after some hours a much denser wall began to form around the larva (Fig. 4D). The larva frequently paused during the construction for up to 2 min. After 20 h the larva ejected its meconium through the circular hole at the bottom of the cocoon. The recently constructed cocoon had a pale-yellow color that turned to orange-yellow over the next day.

All 57 cocoons found were constructed inside the spiders' retreats, but their attachment varied among retreats: 71% were attached to the threads of the tangle near the retreat's roof, 20% were attached to the threads applied by the spider at the apex of the leaf-cone (Fig. 5A), and 9% were in the middle of the retreat, attached to a thick silk cable formed by several independent threads (Fig. 5B).

Enemies of the wasp.—Of the 57 cocoons found, we observed two predation attacks and a possible parasitoid attack on a third cocoon. One pupa was attacked by *Solenopsis* ants inside the spider's retreat. A second pupa or larva inside its cocoon was attacked by a penultimate male of *T. evexum* that fed on the immature wasp through the cocoon silk. The third cocoon had a lateral hole near its bottom that suggested the exit of a parasitoid, as adults of *Z. petronae* exit the cocoon by cutting a circular slit near the cocoon's upper end.

Host spider behaviour.—The spiders carrying first and possibly young second instar larvae (N=4) were capable of capturing prey trapped on the long viscid lines of their webs. Their attack behavior was indistinguishable from the attacks of non-parasitized spiders (Barrantes and Eberhard in prep.). However, spiders with a large penultimate instar or a final instar larva did not attack prey that adhered to the sticky threads. The stickiness of the last capture threads produced by a spider with a large penultimate instar larva was notably reduced, as *Drosophila* flies (with their wings cut) walked easily along these threads.

On four occasions we observed that when a larva apparently bit the cuticle of a spider's abdomen, the spider jerked and tried unsuccessfully to reach the larva with its legs I, II and III. This suggests that the spider perceived and was irritated by the wounds produced by the larva. In one case the spider's leg II touched the anterior portion of the larva, and the larva immediately moved its anterior portion toward

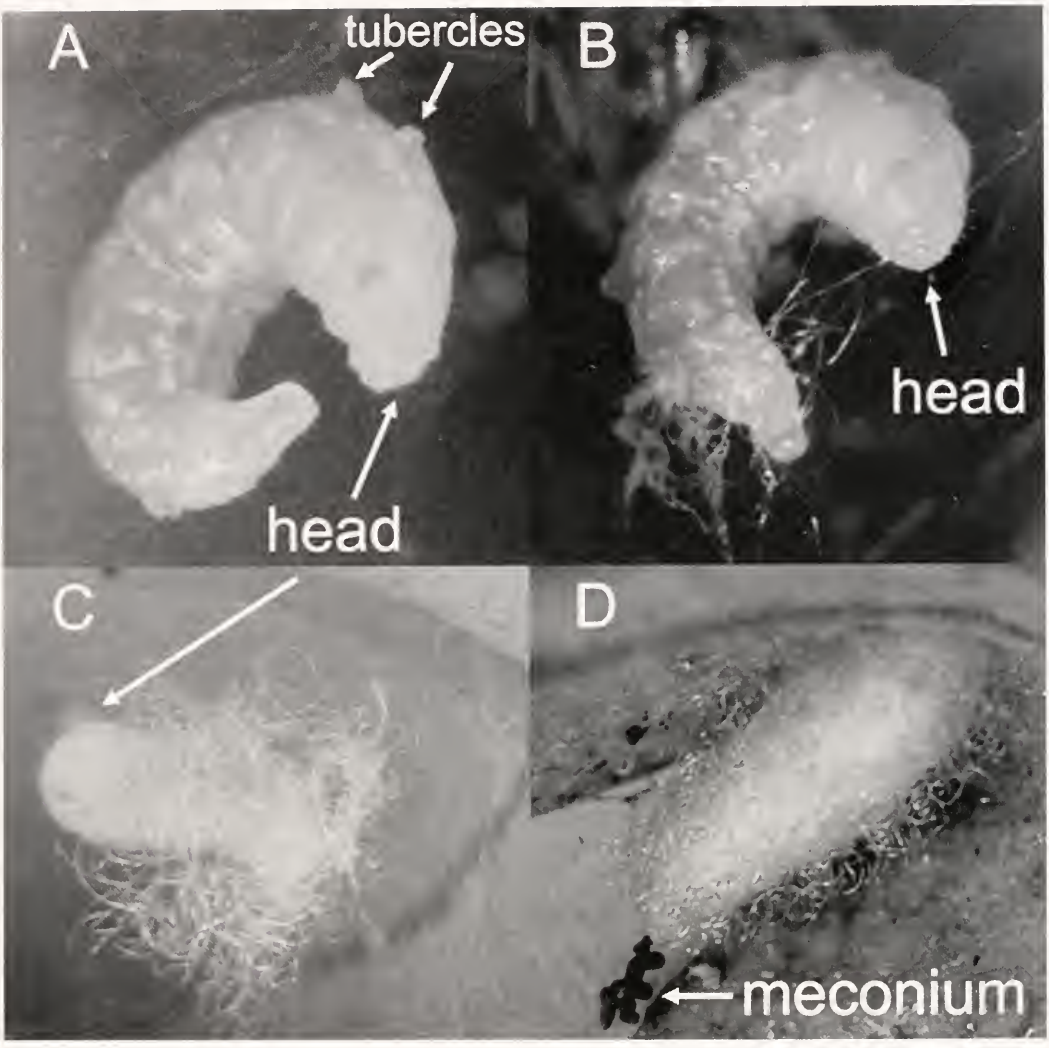

Fig. 4. Sequence of cocoon construction. A) Final instar larva recently freed from the saddle, dorsal tubercles are visible on two abdominal segments. B) Larva about 45 min after cocoon construction began. C) Cocoon construction after approximately 2 h. D) Cocoon after 20 h; note the meconium below the cocoon.

the dorsal-middle section of the spider's abdomen (out of range of the leg) and apparently bit her again. Examination with a hand lens showed that there was a tiny shiny spot, presumably of hemolymph, where the larva had apparently first bitten the spider (documenting that the larva actually bit the host rather than just touched it with its mouthparts is not easy).

The web retreats housing cocoons had additional, non-sticky thick threads either across the retreat opening (72%, n = 57; Fig. 5B), inside, more or less in the middle of the retreat (20%) (Fig. 5B), or both (8%) across the retreat opening and inside it (Fig. 5B). In one case the threads inside the retreat were so dense that they formed a sketchy sheet just below a cocoon (Fig. 5C), which was attached to the tangle threads. A parasitized spider added more threads to the apex of the retreat (Fig. 5A), possibly during the last two nights, before being killed by the larva.

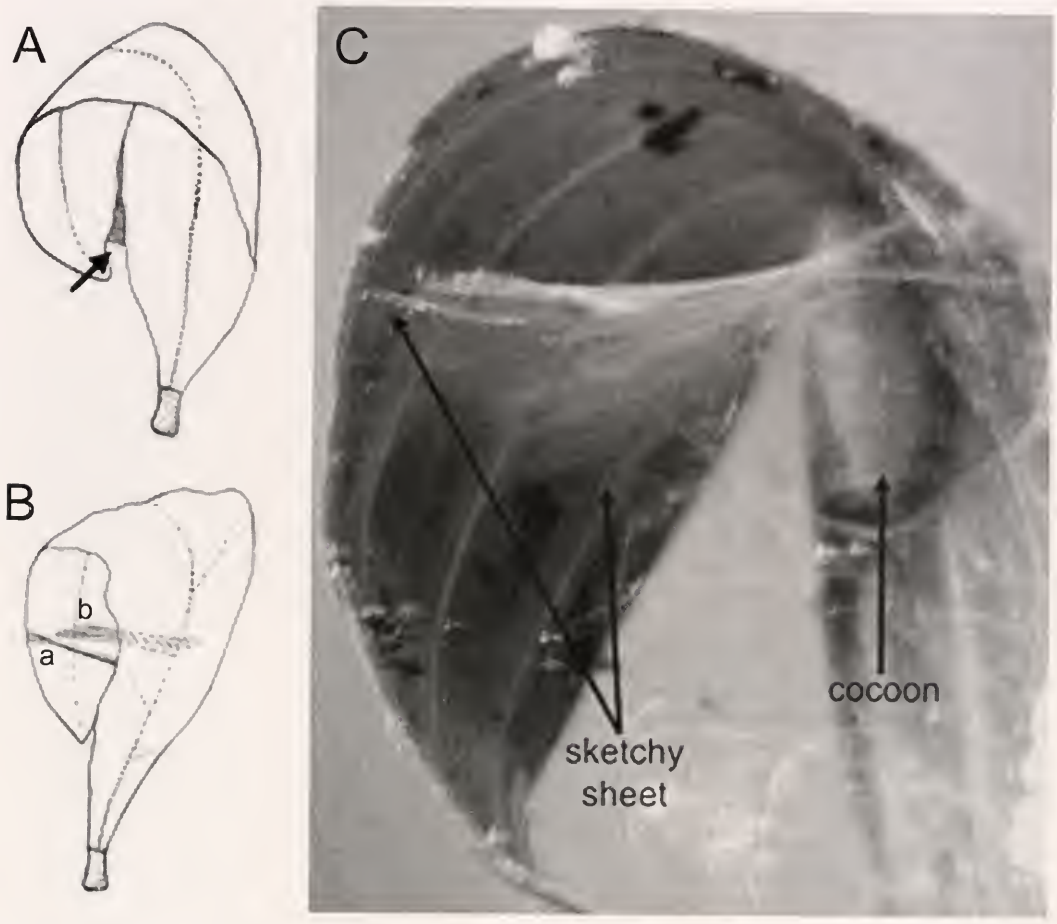

Fig. 5. Retreat constructed by *Theridion evexum*. A) The arrow shows the threads that maintain the leaf-retreat folded. B) Threads added by the spider at the retreat opening (a) and in the middle of the retreat (b). C) Sketchy sheet in the middle of the retreat. Larva of *Zatypota petronae* induces *T. evexum* to produce threads at the retreat opening, inside it and to increase number of threads that maintained the leaf folded (black arrow in A).

DISCUSSION

The morphology and behavior of the larva of *Z. petronae* are quite similar to those of larvae of other polysphinctine species (Nielsen 1923, 1932, Fincke 1990, Gauld et al. 1998, Eberhard 2000a). However, they often differ in where and possibly how their cocoons are attached to the host web. The larva of *Z. petronae* attaches its cocoon, which lacks a suspension line, to silk threads inside the retreat of *T. evexum*, *Hymenoepimecis* spp. attach their cocoon to the spider web (e.g. *N. clavipes* and *P. argyra*) with a suspension line (Fincke et al. 1990, Eberhard 2000a, 2001), whereas the larva of *Reclinervellus nielseni* (Roman) [= *Polysphincta nielseni*] (Nielsen 1923, Gauld and Dubois 2006) and *P. gutfreundi* Gauld (Gauld et al. 1998), which also lack suspension lines, attach the cocoons to the threads near, or on the hub of the orbicular web of *Cyclosa conica* (Pallas) (Nielsen 1923) and *Allocyclosa bifurca* (McCook), respectively. These differences are likely determined by the characteristics of the web of each spider species, particularly by the modifications of the web (the "cocoon web" of Eberhard 2001) induced by the parasitoids (e.g. *T. evexum* re-enforcing its retreat).

There are also differences in how larvae adhere to the saddle. Larvae of *Z. petronae* apparently adhere to the saddle using wedge-like projections of one or two segments, rather than taps as in *Z. albicoxa* and *H. argyraphaga*. Differences may also exist in the sensitivity of the host to the wounds caused by the parasitoid. For example, *P. argyra* did not show any reactions to apparent bites of *H. argyraphaga* larvae (Eberhard 2000a). However, *T. evexum* reacted by jerking its body and moving its legs toward the point where the larva was biting the spider's cuticle. This suggests that chemical composition of secretions could vary among parasitoid species. Further research to confirm chemical differences in the saliva of parasitoids and differences in sensitivity of spider hosts to the bites of their parasitoids is needed.

The release of the saddle by final instar larvae is much more complex than simply the muscular movements of the posterior end of the larva as suggested by Nielsen (1923) and Eberhard (2000). Without the powerful pressing and pushing movements of the larva against the saddle, the peristaltic abdominal movements are possibly insufficient to free it from the saddle. More information is needed to examine the possible differences among polysphinctine species.

The larva of *Z. petronae* induces the host spider to add more threads on different sections of the retreat (apex, inside, and across the retreat opening) that make this structure stronger and more durable. Adding threads near the apex of the retreat is apparently a repetition of a subroutine used in the construction of the retreat by an unparasitized spider, since threads applied in similar fashion allows the spider to fold the leaf and maintain the retreat's shape. Similarly, threads across the retreat opening were occasionally present (3 out of 17 webs) when pre-adult female spiders were molting, though these threads were not as abundant as those in retreats of parasitized spiders. However, the thick cable of silk threads produced inside the retreat was not found in webs of unparasitized spiders. The reinforcement of the retreat with additional silk threads possibly increases the protection of the cocoon, primarily against heavy rains, which is likely important for the wasp's survival. If a retreat opens up, it is unlikely that the thin threads of the tangle inside the retreat, where most cocoons were attached, could survive heavy rains intact.

Our observations suggest that *Z. petronae* is not specialized on a particular species of host. This wasp parasitized intermediate sized spiders (at least 4th instar), but the reproduction of *T. evexum* is highly seasonal and large juvenile spiders occur only during five or six months of the year. Thus, it is likely that *Z. petronae* must parasitize at least one other species of spider to maintain its population.

The percentage of parasitism of *T. evexum* (1.39% ± 1.80) was relatively low when compared with other spider species. Fincke et al. (1990) reported that the annual percentage of parasitism for intermediate-sized juvenile females of *N. clavipes* was 15–30%, and Eberhard (2000) reported that the parasitism on *P. argyra* was higher than 40% for mature females and higher than 3% for mature males. The low parasitism on *T. evexum* also suggests that *Z. petronae* is possibly using other spiders as hosts in the same area.

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